POPULATION ECOLOGY AND LIFE-HISTORY TACTICS OF SHALLOW, SAND-BOTTOM CRUSTACEANS AT KAIKOURA

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CONTENTS

ABSTRACT

Quantitative random sampling of a shallow, sand bottom exposed to unpredictable storm wave action at Kaikoura, New Zealand, between Oct. 1978 and Oct. 1980 provided detailed information on the population biologies of five crustaceans, the large myodocopid ostracod *Cycloleberis zealandica*, and the gammaridean amphipods *Hippomedon whero*, *Patuki roperi*, *Metaphoxus littoralis* and *Paraphoxus australis*. Data for each species included seasonal changes in population density and structure, cohort composition, age at maturity, longevity, frequency and occurrence of breeding, egg size, duration of embryonic development, brood size and mortality, number of instars and broods per life-time and population sex ratios. The biology of myodocopid ostracods is reviewed and discussed with respect to *Cycloleberis* and the question of instar size variations in ostracods generally is explored. Results for the amphipods are discussed in relation to current knowledge of amphipod biology.

Utilization of the sand habitat was examined by comparing species population densities and compositions in ripples and in troughs at different times. Species sediment-depth distributions in ripples and in troughs were investigated in two successive months by sectioning cores into five layers. In some species juveniles, males and females inhabited different depths and other species were more abundant in either ripples or troughs. Sediment depths inhabited are discussed with respect to species burrowing rates, food, and an optimal sediment depth where niche overlap, and presumably competition also, is greatest.

Recolonization of defaunated sand by each species was monitored over 1, 4, 8, 16 and 26 days initially and over 1 and 26 - 39 days during each of five subsequent months. Initial results showed remarkably fast recolonization by some species and changes in species population densities as recolonization proceeded. Within species the relative recolonization rates of juveniles, males and females may differ along with the sizes of recolonizing and control species subgroups. However, the experiments in subsequent months revealed that the pattern of species recolonization may change with time in response to no obvious factors.

Results of the preceeding chapters are brought together in a final discussion of crustacean life-history tactics. Sediment depths inhabited

provided a ranking of species habitat stabilities and mortality risks, both greatest at the sand surface. Population parameters, including net reproductive rates and innate capacities for increase, confirmed the ranking, but comparisons with species combinations of life-history traits strongly disagree with the predictions of two theories, r- and K-selection and bet-hedging. The failure of these theories is principally due to the existence of phylogenetic constraints, the lack of viable genetic alternatives for a trait. A new theory is required that encompasses phylogenetic constraints and recognizes the possibility of several equally successful combinations of traits in a given situation. Such a theory based on established ideas of costs of reproduction and of larger offspring from larger eggs being ecologically fitter must incorporate recent ideas on growth rates, body size and size-specific mortality.

CHAPTER 1

INTRODUCTION

Perhaps no field of biology attracts such wide attention as the study of life-history tactics where a single theory which permits reliable prediction of the combinations of life-history traits for organisms occupying variously stable or unstable habitats is still being sought. Surprisingly, only two theories have enjoyed popular support, r- and K-selection (MacArthur & Wilson, 1967; Pianka, 1970a) and bet-hedging (Murphy, 1968; Schaffer, 1974b). The former predicts that organisms experiencing wide fluctuations in population density, high density-independent mortality or repeated colonization tend to evolve a combination of earlier maturity, larger broods, higher reproductive effort, and shorter lifespans than organisms exhibiting constant population density or subjected to density-dependent mortality. The latter theory, bet-hedging, predicts that fluctuating environments that cause high prereproductive (juvenile) mortality favour reduced reproductive effort, smaller clutches, and longer lifespans, whereas increased reproductive effort, larger clutches, and shorter life-times are favoured where environmental fluctuations affect adult (reproductive) survival. Stearns (1976, 1977) reviewed the development of these ideas and, after reviewing available data, concluded that "We do not yet have a general and reliable theory of life history evolution" and further, that parameters appropriate for the basis of such theory remained unidentified. Subsequently little has changed. More emphasis has been placed on quantification of reproductive costs (Bell, 1980) but this has produced no panacea. Thus it seems that theoretical development has proceeded too far and now it is time to look at the organisms again in search of new insights. Three factors have emerged since Stearns' (1976, 1977) reviews.

First, it is immediately obvious to specialists of many invertebrate groups that little or no variation is possible for some life-history traits. For example, all myodocopid ostracods are semelparous. Thus following either theory, myodocopids must inhabit fluctuating environments, an untenable conclusion. Several workers have noted that presence of such phylogenetic constraints (see Chapter 12 for definition) (Christiansen & Fenchel, 1979; Reaka, 1979, Lynch, 1980) but apparently their importance in at least some invertebrate taxa has been largely ignored. For this reason then, comparisons of life-history tactics

should be made within taxa subjected to similar constraints. Thus Reaka (1979) confined her attention to stomatopod Crustacea of the family Gonodactylidae and Lynch (1980) compared species from five families of Cladocera.

The second factor is: Specific life-history traits are correlated with body size in different taxa. For example body size is correlated with egg size and juvenile settling size in gonodactylid stomatopods (Reaka, 1979) and female size at maturity is correlated with brood size in gammaridean amphipods (Chapter 9). Therefore the traditional life-history traits (egg size, brood size, juvenile size, length of life) alone seem to be inappropriate parameters for comparing life-history tactics.

Thirdly, Lynch (1980) explored the implications of body size with respect to optimal foraging size, size-specific predation and reproduction, convincingly demonstrating that predation has a very pronounced influence on body size and on reproductive tactics in Cladocera.

Thus the student of life-history evolution is now faced with the rejection of the established theories, the presence of various limitations of life-history trait options available in different taxa, the inter-related nature and hence inadequacy of several more obvious traits, and the introduction of previously unrecognized selective pressures.

The present study began before much of this information was available and so must be excused for not encompassing all of these factors. Indeed the study was conceived as a detailed investigation of the life-history tactics of five crustaceans (four gammaridean amphipods and one myodocopid ostracod) coexisting in an unpredictable habitat. Its basis is a knowledge of the reproductive and population biology of each species which ultimately lacked the desired thoroughness, probably because I attempted to encompass too many species. Despite this, the ecological work has proven interesting and given rise to some thoughts on the question of life-history tactics.

During the course of this work four publications appeared each reviewing, in its own way, the biology and life-history patterns of gammaridean amphipods: One reviewed the reproductive biology of British amphipods (Moore, 1981); two attempted to analyse the life-history patterns of gammarideans (Nelson, 1980; Van Dolah & Bird, 1980) but considered too few traits; while the most recent paper (Wildish, 1982) provided a superficial review of life-history patterns,

factors affecting their evolution and of costs of reproduction. My discussion of amphipod life histories (Chapter 9) is intended to put the Kaikoura species in perspective and does not attempt a comprehensive treatment of the field.

In addition to the population biologies of each species, I investigated the microdistribution of each species (Chapter 10) and their rates of recolonizing defaunated sand (Chapter 11) to provide information on the relative stabilities of their habitats and on species mobilities, information of considerable value in the final discussion of life-history tactics (Chapter 12). Two species of amphipods examined in this study proved new to science and these have been described in the course of this work (Fenwick, in press).

CHAPTER 2

METHODS

The study area was in South Bay, Kaikoura, (Fig. 3.1) and consisted of a patch of coarse shelly sand about 15 m diameter in 6 m of water. A bouy was anchored above this for ready location of the site and as a means of maintaining a boat on station. All sampling and other work was done by diving using either scuba or a surface operated compressor with an airline to the diver. I took all samples and on occasions other divers helped with additional work.

At approximately monthly intervals between Oct. 1978 and Oct. 1980 populations of crustaceans inhabiting the sand were sampled by taking six to eight replicate cores of sand; on one occasion rough weather resulted in the collection of only four cores. Cores were taken to 187 mm sediment depth using coffee cans with a cross-sectional area of 0.0125 m^2 or $^1/80$ m^2. These cans were completely open at one end and closed at the other except for a 'window' of very fine (0.1 mm) brass mesh which prevented washing of the sediment as the corer was worked into the uncompacted sediment by hand. Full cores were removed from the sediment by digging down beside the corer and placing a hand over the open end. They were immediately inverted, placed in individual plastic bags, sealed and kept inverted until processed in the lab. Rarely the corers struck rock before penetrating to their maximum depth and such samples were re-taken. During the second year an additional set of eight cores was taken at each time and these were placed together in a mesh (0.5 mm) bag to remove smaller animals and much of the sand. After taking this set of cores the mesh bag was sealed in a plastic bag and taken to the laboratory.

Samples were located using two-digit random numbers. On arrival at the station a flat iron weight (bouyed) with ten numbered (0-9) radial lines was dropped to the bottom. On the bottom the first random digit indicated a direction from the weight corresponding to a radial line and the second digit determined the distance from the weight in 0.5 m intervals along a graduated line. One core was taken at each point and another random number consulted for the next sample.

Samples were processed at the Edward Percival Field Station (E.P.F.S.) (Department of Zoology, University of Canterbury), Kaikoura, within three hours

of collection. Crustaceans were removed from each core by agitating the sample in a mixture of kerosene and water (sufficient water to cover the sand by about 40-50 mm and a 1-2 mm layer of kerosene) and decanting the supernatant through a fine (0.25 mm) sieve until no further animals appeared in the residue on the sieve, usually four to six times. Hydrocarbon flotation is a well-known method of extracting arthropods from soils (Southward, 1966) and carbon tetrachloride is usually used. Kerosene is a cheaper and safer alternative. Although some sand and organic detritus was included with the extracted fauna, the method was very efficient and reduced the volume of material for manual sorting from 2360 cm^3 to about 50 cm^3. Table 2.1 provides an indication of the method's efficiency. The material (including animals) retained on the sieve was washed in 70% alcohol and tapped gently several times to remove most of the kerosene before preserving in alcohol in labelled jars.

Subsequently, all crustaceans were extracted and sorted into species by searching each sample using a stereomicroscope at 16X magnification. Later, each sample was counted, measured, sexed and the development of any embryos found recorded following Thurston (1968), Bregazzi (1973) and Fish (1975):

Stage 1, undifferentiated or close-packed yolk cells with no trace of embryonic tissue.
Stage 2, early embryo with no obvious structure, surrounded by embryonic membranes.
Stage 3, embryo with obvious somites and limb buds.
Stage 4, late embryo in which development is almost complete, eye pigment present, still within membranes.
Stage 5, fully developed juveniles hatched and free in the brood pouch.

The number of embryos was recorded for each brood along with the length of three randomly chosen embryos. In some instances widths and heights of embryos were also measured.

All measurements were made using an eyepiece micrometer in a stereomicroscope. For the amphipods, these were made at 40X magnification in units of 0.025 mm and measurements of ostracods were made at 16X magnification to the nearest 0.0625 mm. The size of individual amphipods was measured from the left side as the length of the head from anterior-most margin (tip of

Table 2.1 Numbers of crustaceans extracted from four sand samples by kerosene flotation and by subsequent manual sorting (in brackets).

	Samples			
	1	2	3	4
Cycloleberis zealandica	12(0)	24(0)	24(0)	14(0)
Amphipoda (5 spp.)	100(0)	40(0)	140(0)	109(0)
Exosphaeroma sp.	1(1)	8(0)	28(0)	2(0)
Maoridotea naylori	2(0)	0(0)	1(0)	2(0)

rostrum in all except one) to the posterodorsal margin (displacement of peraeonite 1 was often necessary to expose this). Total length is difficult to measure in amphipods and subject to considerable error because their bodies are variously flexed when dead. Various workers (e.g. Cooper, 1965; Mathias, 1971) used head length whereas others (e.g. Moore, 1981) continue to use total length. To facilitate comparisons between published accounts of other species, I measured both dimensions for several individuals and determined linear relationships between them for all species. Regression equations describing these relationships and their significance are given in Table 2.2. Sizes recorded for ostracods were lengths of their left valves measured from the anterior margin of the rostrum to the posterior margin.

Amphipods were classed as male if penes were apparent between the bases of their seventh peraeopods, or as females if oostegites were present medially on the bases of any peraeopods. Individuals lacking either penes or oostegites were considered juvenile. Ostracods were sexed by examining the condition of the antenna 2 endopod: In females, the endopod is small, the terminal third article is small relative to the subequal first and second articles and bears a single seta apically. The endopod increases in relative size with successive instars in males, article 3 increases in size relative to articles 1 and 2, and the single subterminal seta is inserted proportionately closer to article 2 (see Kornicker & Maddocks, 1977 for illustrations). I could not sex individuals in their first three instars by this method and

Table 2.2 Relationships between total body length (Y) and head length for the four Kaikoura amphipods (model 2 regression).

Species	Regression equation	r	p	n
Hippomedon whero	Y = 0.0820 + 0.0702X	0.972	<<.01	117
Patuki roperi	Y = 0.1693 + 0.1020X	0.955	<<.01	37
Metaphoxus littoralis	Y = 0.0885 + 0.1645X	0.983	<<.01	46
Paraphoxus australis	Y = 0.1052 + 0.1505X	0.988	<<.01	50

these were considered to be juveniles.

Live animals required for various experiments were collected at the study site from time to time by scooping sand into a bucket and transporting this to the lab. immediately. The sand was covered with seawater at all times and maintained in running seawater at the lab. Individuals for growth experiments were held separately in plastic, screw-top jars with mesh ends, similar to those described by Hardy (1978), and containing a small amount of sand from the habitat. These were kept indoors in tanks of flowing seawater at E.P.F.S. Water temperatures were similar to ambient sea temperatures although diurnal fluctuations of up to 5°C did occur on hot, sunny days. The bottoms of these tanks were covered with 20-30 mm of sand taken from the study area but with the larger crustaceans removed. Cultures were checked at monthly intervals when small quantities of dried cereal (baby food) were added to each jar.

Experiments to determine embryonic development times were undertaken in the Department of Zoology, Christchurch. Again individuals were kept in mesh-ended plastic jars containing a little sand. These were immersed in filtered seawater in plastic trays and maintained at 15°C with a 12 h light/dark cycle in constant temperature cabinets. Water in each tray was aerated continuously and replaced with fresh, filtered seawater every two days. Minute amounts of dried cereal were added every few days to provide a food source. Cultured animals were examined and measured alive while in a shallow dish of seawater.

Reliable measurements were possible but I could not sex individuals or examine broods in living animals.

Samples of sand at the study site were collected irregularly by scooping sand from the surface 50 mm into a jar. Subsequently these were analysed for particle size composition in the Department of Geography, University of Canterbury, by dry sieving.

Surface water temperatures were taken monthly at the study site, but temperatures measured weekly by Mr J. van Berkel at the New Wharf, Kaikoura, provided a better record of seasonal changes. Wave height data used in the study were collected by the Kaikoura Meterologist and generously supplied by the New Zealand Meteorological Service, Wellington. On occasions I witnessed some storm events but made subjective notes on them only.

CHAPTER 3

STUDY AREA

The Kaikoura Peninsula (centred on 42° 25' S, 173° 42' E) (Fig. 3.1) is located on the north-east coast of the South Island and projects seaward 4.5 km perpendicular to the north-east - south-west coastline. It consists of intensely folded limestone and mudstone, and its compact shape is broken by projecting points and small bays. Two such bays situated on the Peninsula's south-west coast are Limestone Bay and the adjacent Mudstone Bay, separated by a long, broken ridge of submerged and emergent limestone bedrock known as Baxter's Reef. The bottom of Limestone Bay slopes gently seaward and towards Baxter's Reef where it is broken by a few channels. It consists mostly of cobbles, and exposed, rounded humps of bedrock but, there are large patches of clean, white sand in the vicinity of channels through the Reef. The site chosen for this study was one such patch of sand, about 15 m diameter at about 6 m depth and within the largest opening in Baxter's Reef (Fig. 3.1). To seaward the bottom changes to dissected bedrock separated by occasional very small sand patches and, beyond the reef, it slopes downward moderately steeply.

Kaikoura Peninsula is exposed to high energy oceanic swell and storm waves emanating from the south, south-east and north-east. Storm wave action is more intense and more frequent on the southern coast with waves larger than 1.5 m occurring about 15% of the time (Kirk, 1977). Thus the wave environment of the southern coast and the study site comprises protracted intervals of small waves and low swell (<0.5 m high) interrupted by periods of intense storm-wave (>2 m high) activity at any time of the year depending upon cyclonic conditions (Kirk, 1977). During severe storms the shallowing bottom causes waves to crest and break over the study area resulting in intense sediment movement as evidenced by large (200 mm high) ripple marks, deep scouring around rocks and occasional complete burying of low bedrock exposures.

Figure 3.2 shows the mean monthly frequency of different sea-state (wave height) classes at Kaikoura for five years (data from McLean, 1968; Kirk, 1972, 1973, 1974, 1975). Subjectively there is no marked seasonality of storm waves (classes 4-5, waves >1.25 m high) although Stephen (1974) reported a slight winter increase in the frequency and height of waves from

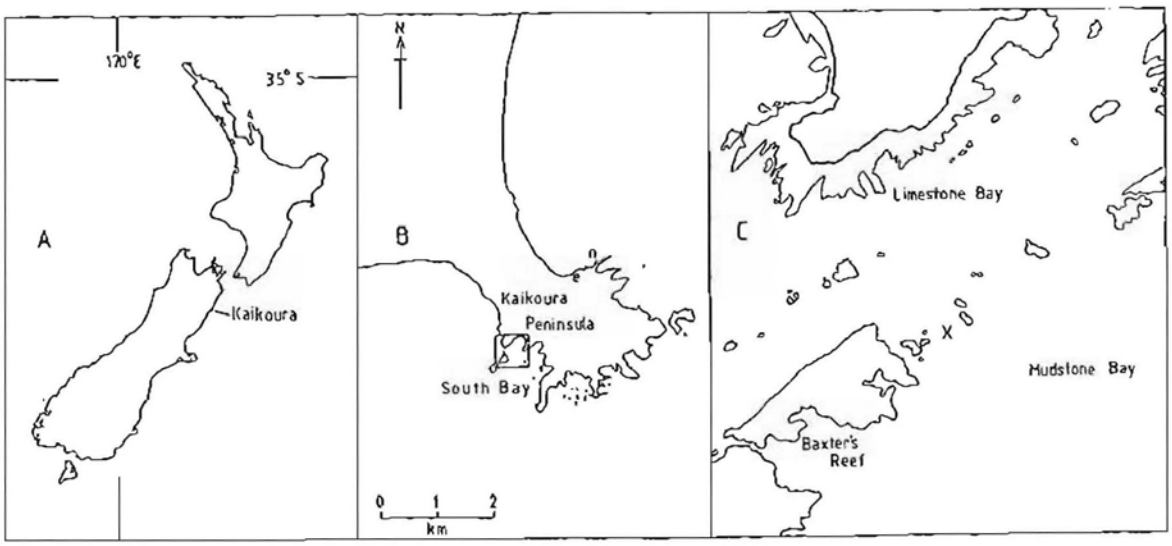

Fig. 3.1 South Bay study area: A, New Zealand; B, Kaikoura Peninsula, inset shows portion of South Bay investigated (e, Edward Percival Field Station; n, New Wharf); C, study site (x).

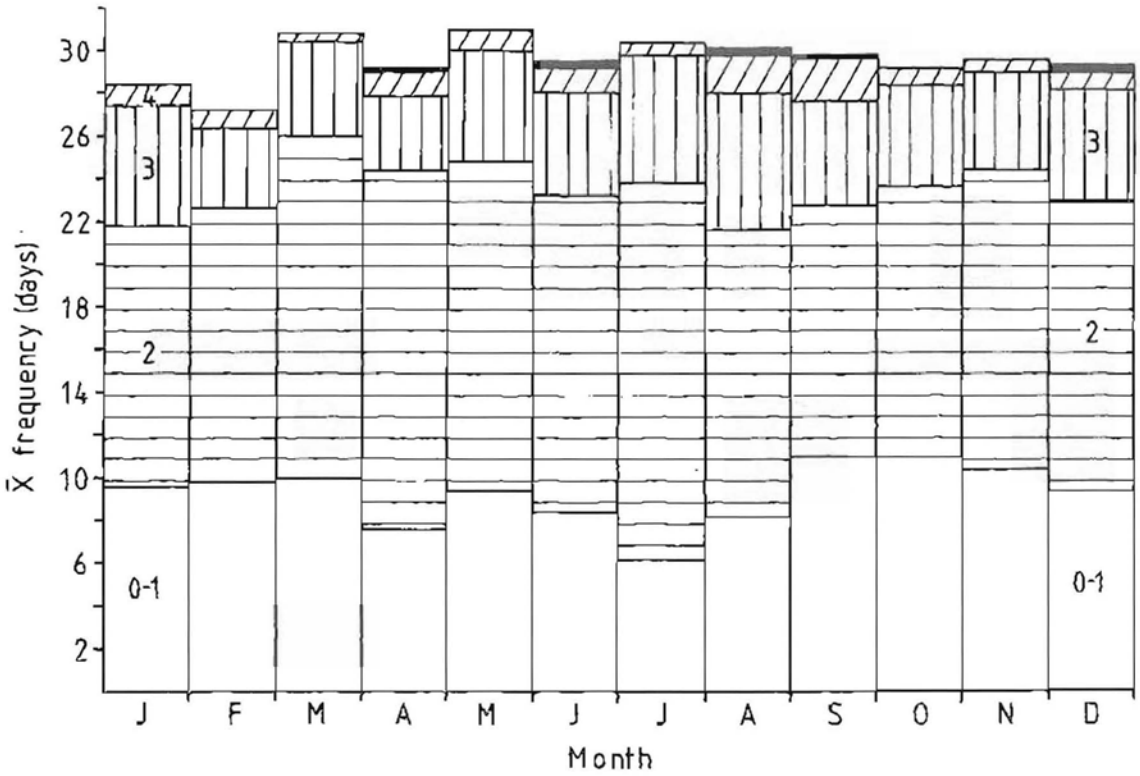

Fig. 3.2 Mean monthly frequencies of wave heights (troughs to crests) at Kaikoura for 1967 and 1971-74. 0, calm; 1, waves <0.1 m; 2, wavelets, 0.1-0.5 m; 3, slight, 0.5-1.25 m; 4, moderate, 1.25-2.5 m; 5 (black), rough, 2.5-4 m.

the south. The occurrence of waves >2.5 m high is usually infrequent (five times in five years). During this study, however, storm waves were concentrated between July and Feb. and in the 1979-80 summer there were several days of storm waves (Fig. 3.3) including one day with waves exceeding 2.5 m high.

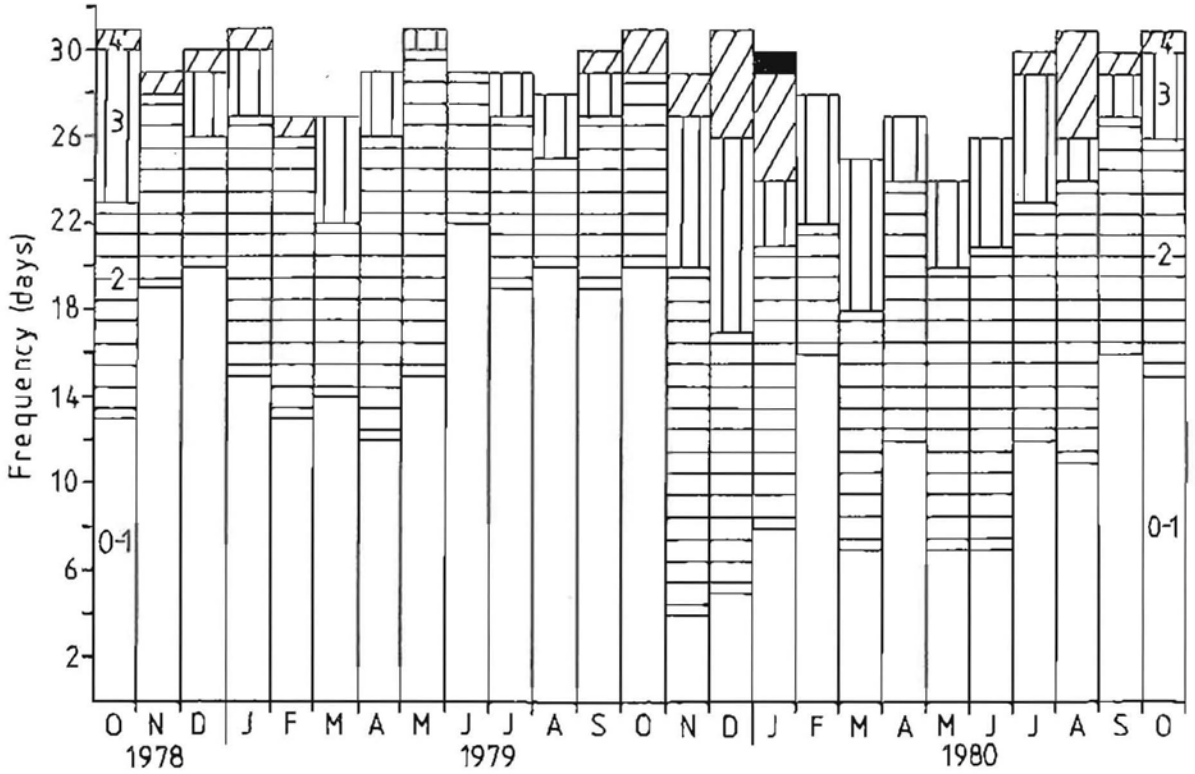

Fig. 3.3 Monthly wave heights at Kaikoura during Oct. 1978 - Oct. 1980.

Inshore sea-surface temperatures ranged between 8.8 and 18.0°C (Fig. 3.4) for the period Oct. 1978 - Oct. 1980. Ottaway (1976) reported a slightly wider range of 8.5 to 19.0°C, probably because he recorded temperatures of waters very close (within 1 m) to rocky shores whereas the readings for Fig. 3.4 were taken at the seaward end of the New Wharf, Kaikoura (Fig. 3.1). Both sets of data show the same seasonal temperature pattern of a steady increase from the winter minimum in Aug. to a summer maximum during Dec.-Feb. followed by a more gradual decline to winter temperatures. Distinct differences occur from year to year in the timing of certain temperatures, especially the summer maxima, and in the duration of warmer or colder periods.

The bottom at the study site consisted of well-sorted medium sand with mesokurtic (normal), near symmetrical sorting or skewness (verbal classification following Folk, 1965) (Table 3.1). Seasonal changes of the sedi-

Table 3.1 Description measures (phi notation) of sediment at the study site at different times: Median sediment type (Wentworth scale), graphic mean particle size (M_z), inclusive graphic standard deviation (σ_I), inclusive graphic skewness (SK_I) and kurtosis (K_G) (all values positive).

Date	Median sediment type	$M_z(\emptyset)$	$\sigma_I(\emptyset)$	SK_I	K_G
12 Nov. 1978	medium sand	1.525	.371	.057	.992
1 Jan. 1979	medium sand	1.325	.438	.031	1.070
4 Feb. 1979	medium sand	1.355	.440	.083	1.118
9 Mar. 1979	medium sand	1.405	.451	.063	1.238
28 Apr. 1979	medium sand	1.385	.507	.100	.998
3 July 1979	medium sand	1.295	.448	.052	1.074
11 Aug. 1979	medium sand	1.605	.361	.075	1.033
8 Sept. 1979	medium sand	1.385	.440	.075	1.095
9 Nov. 1979	medium sand	1.095	.454	.109	1.102
6 Dec. 1979	medium sand	1.610	.360	.110	.995
23 Jan. 1980	medium sand	1.545	.443	.004	1.021
29 May 1980	medium sand	1.325	.416	.111	1.070
28 Aug. 1980	medium sand	1.630	.416	.016	1.036

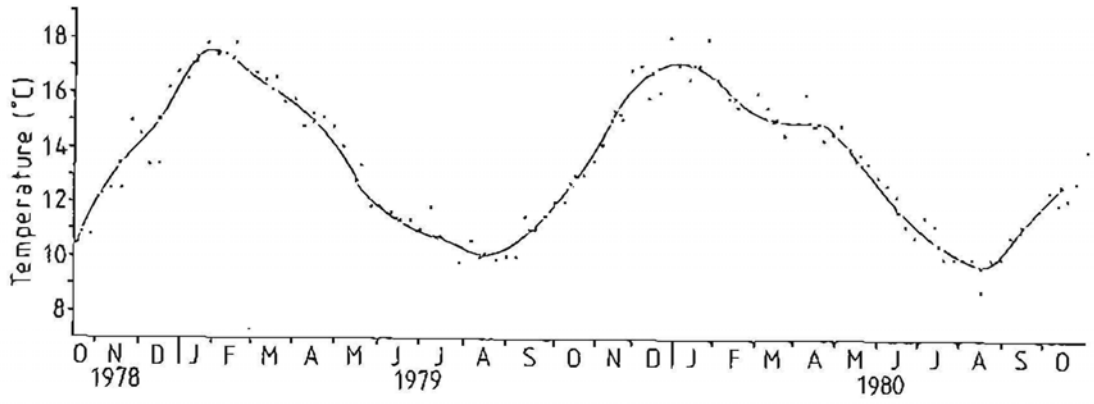

Fig. 3.4 Weekly and mean monthly sea surface temperatures recorded at the New Wharf, Kaikoura (courtesy Mr B. Shakespeare (N.Z. Oceanographic Institute), data collected by Mr J. van Berkel (E.P.F.S.).

ment were minimal for all measures (Table 3.1). Microscopic examination revealed that the sand particles (0.125 - 2.000 mm) consisted almost entirely of calcium carbonate plant and animal remains. Identifiable particles consisted of fragments of bivalve and gastropod shells, echinoderm plates and spines, Foraminifera, pieces of bryozoan colonies, and of coralline algae, barnacle plates, polychaete tubes and abundant micromollusc shells. Organic detritus was common within the sediment and occasionally occurring in dense layers. At times detritus accumulated in the troughs of ripples when, especially after storms, it consisted principally of algal fragments. Detritus found within the sand consisted mainly of woody twigs, beetle elytra and seeds of higher plants, all of terrestrial origin and probably transported via the Kowhai River, some 4.5 km to the west. No attempt was made to measure the quantities of organic detritus present because of the high carbonate interference inherent in most methods when working with such sand (Byers *et al.*, 1978).

Apart from the five crustaceans examined in this study, other inhabitants of this habitat were either not abundant or inconspicuous. Crustaceans found included several large *Maoridotea naylori*, abundant juveniles of *Exosphaeroma* sp., an unknown idoteid isopod, about six species of amphipods, about eight species of ostracods, various harpacticoid copepods, mysids, a nebaliacean, three species of Cumacea, and rarely hermit crabs and *Ovalipes catharus*. Nematodes were extremely abundant in some samples but apparently

absent from others. Examination of two samples in detail revealed 14 species of polychaetes with *Hemipodus digitifera* the most common species. An unidentified oligochaete was also abundant. Occasional juvenile ophiuroids were found along with a few small holothurians, probably *Chirodota mortenseni*. No large molluscs were present and few of the abundant micromollusc shells contained live animals. One small fish, *Tewera cranwellae*, was moderately common and burrowed into the uncompacted sand. Various other fishes were seen over the study site but are not true inhabitants of the sand habitat.

A notable feature of this fauna is that all species live freely in the sediment and none builds any semipermanent or permanent burrow. Indeed from above, the rippled sediment surface appears devoid of life, completely lacking tubes or burrows.

CHAPTER 4

THE BIOLOGY OF *CYCLOLEBERIS ZEALANDICA* (BAIRD, 1850) (OSTRACODA, MYODOCOPIDA)

INTRODUCTION

Ostracods of the order Myodocopida are important members of the benthos and plankton of most oceans but they have received little attention apart from taxonomic studies. Very few published accounts describe in detail the reproduction and life histories of myodocopids. This is the first study of the life history and population changes of a myodocopid ostracod by regular sampling of one population, an approach widely used in the study of other crustaceans.

Cycloleberis zealandica is a large, benthic species reaching about 5.5 mm long in its final, sexually mature instar. Adult males possess very elongate first antennae, the second antennal endopod is modified into an elaborate clasping organ, the carapace is more elongate than the female's and it is encircled by a vertical row of long, fine setae towards the posterior as in *Cycloleberis christiei* (Kornicker & Maddocks, 1977). Adult females lack such modifications but are slightly larger than males, and incubate their bright orange eggs within the posterior half of the carapace and overlying the lamellate gills. By day, all instars live in the coarse sand bottom, but during darkness they may be found free-swimming in the water above.

POPULATION BIOLOGY

DENSITY

The *Cycloleberis* population in South Bay undergoes marked seasonal fluctuations in mean density (Fig. 4.1) from a winter low of 19 0.1 m^{-2} to almost 350 0.1 m^{-2} in summer. A regular pattern of highest density in Dec. - Jan. declining to a lowest density in July - Aug. is immediately apparent, but the density changes are not gradual. Further, the timing and magnitude of major peaks and troughs vary slightly from year to year. Most importantly, however, there is a single annual peak implying a single summer recruitment to the population.

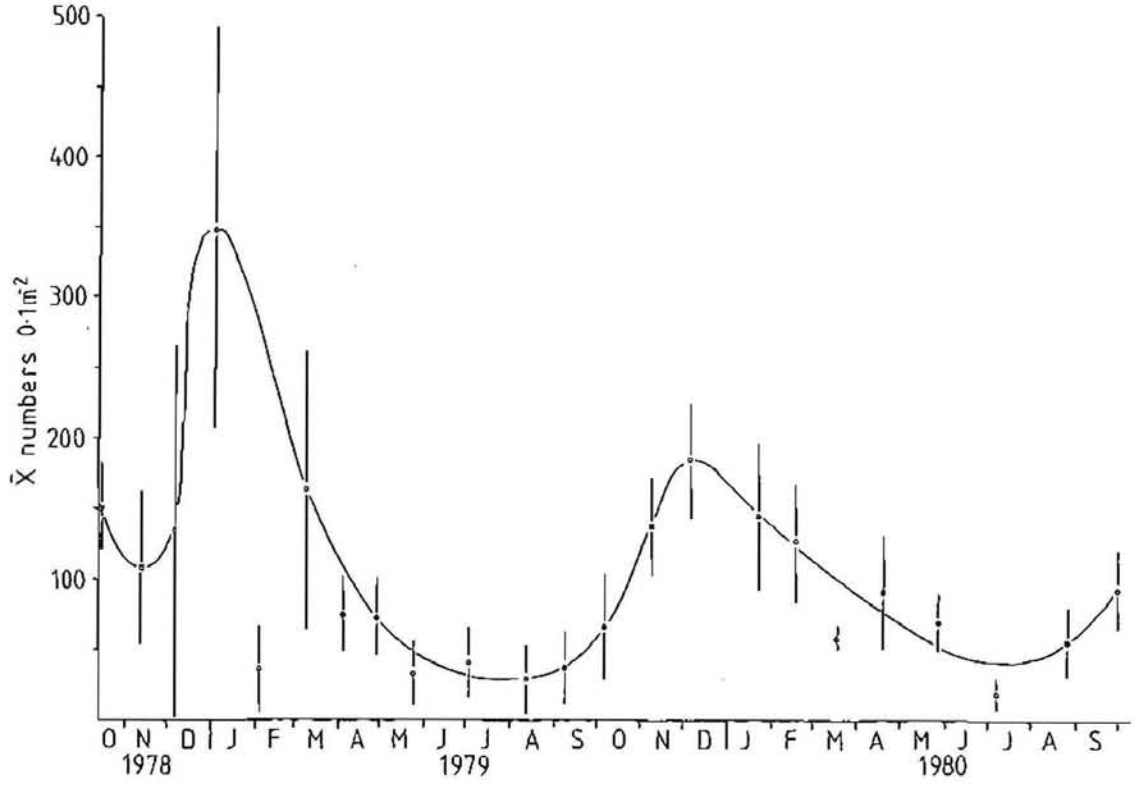

Fig. 4.1 Mean monthly densities (±2SE) of *Cycloleberis*.

INSTARS

Cycloleberis undergoes seven instars as seen in Fig. 4.2, a length-frequency histogram for all individuals taken during the study. Instars are discrete, sexes can be distinguished fairly reliably from instar IV and males are slightly larger than females in all but the final instar. The few adult (instar VII) males collected were smaller than adult females. Table 4.1 summarises these data and a series of t-tests shows that the length difference between sexes of the same instar is highly significant.

SEX RATIOS

The overall sex ratio (♂:♀) observed for *Cycloleberis* was 0.584 (Table 4.2), that is, almost two females for each male. However, the sex ratios are at parity in instars V and VI and they deviate significantly in instars IV and VII. Individuals were sexed by inspection of the antenna 2 endopod, a difficult task in small fourth instar individuals. The apparent deviation of this instar's sex ratio probably results from misidentification of females

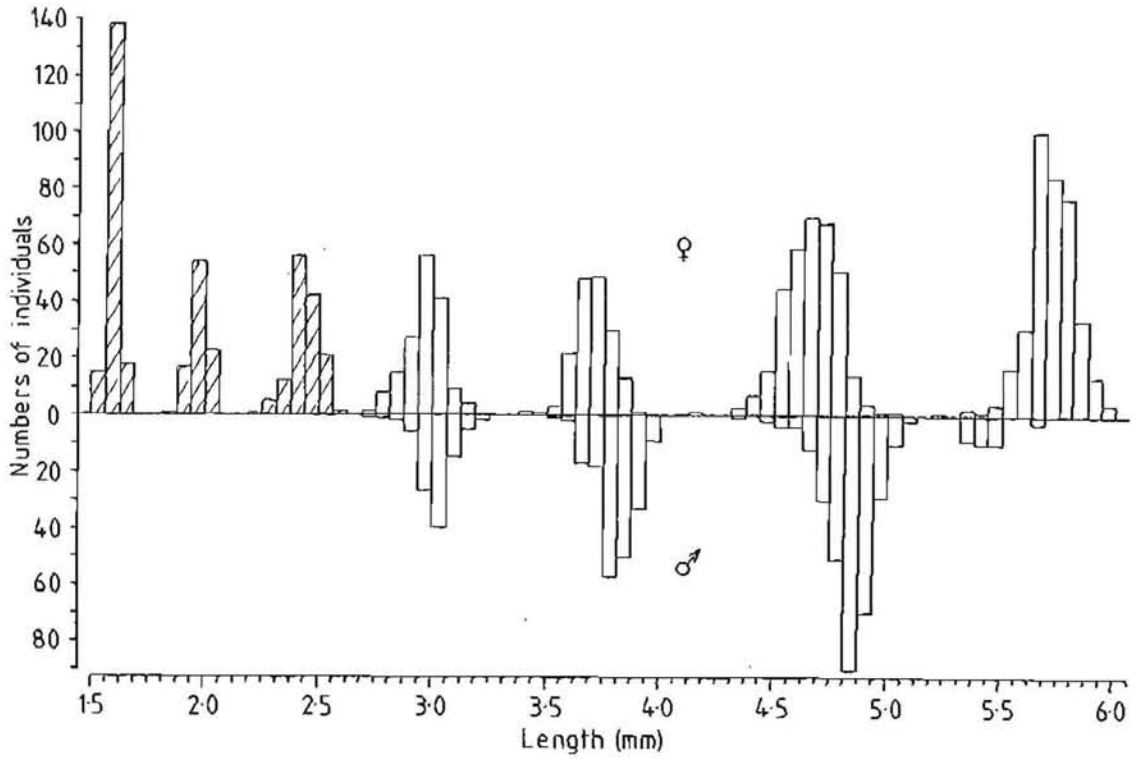

Fig. 4.2 Length-frequency distribution of all *Cycloleberis* individuals collected Oct. 1978 - Oct. 1980.

because sex ratios in the two succeeding instars are 1:1. Consequently, sexes of this instar will not be distinguished in the following results. Very low numbers of instar VII males cause the highly disparate sex ratio observed. Again, this is evidently a sampling error since sexes are equally abundant in the two preceeding instars and at the time of moulting from instar VI to instar VII the number of males almost certainly equals that of females. This relatively great scarcity of adult males has been widely reported for myodocopid ostracods (Elofson, 1941; Hulings, 1969; Kornicker, 1969; Baker, 1978). Along with the morphological changes associated with the sexually mature final instar found in the genus *Cycloleberis* and in other myodocopid ostracods, there is an apparent change in habitat. Many authors considered that the change in male antennal morphology at the final moult prevents continuation of the burrowing habit and marked the onset of a pelagic phase. Both males and females kept in cages containing sand in the laboratory were usually found buried in the sand rather than at its

Table 4.1 Mean lengths (mm), standard deviations and significance of sexual size differences of each instar of *Cycloleberis* from South Bay, Oct. 1978 - Oct. 1980.

instar		$\bar{x}$ length (mm)	SD	n	Significance
I		1.562	0.023	171	
II		1.944	0.037	95	
III		2.406	0.065	138	
IV	♂	2.987	0.078	99	t = 5.093, dfs = 258
	♀	2.935	0.083	161	p <<.001
V	♂	3.778	0.086	187	t = 12.256, dfs = 353
	♀	3.670	0.080	168	p <<.001
VI	♂	4.805	0.109	310	t = 20.672, dfs = 647
	♀	4.624	0.114	339	p <<.001
VII	♂	5.403	0.090	21	t = 13.725, dfs = 380
	♀	5,682	0.101	371	p <<.001

surface or swimming in the water above. Tests (Table 4.3) showed that their burrowing rates are similar to those of adult females and other instars. However, the general scarcity of adult males in sand samples and their abundance (21♂:12♀) in a single night plankton tow (8 May 1980, 2030 h) indicate a change in habitat. In his study of the Sarsiellidae, Kornicker (1969) discounted a habitat change by adult males "because of the absence of records of collections of sarsiellids in which males are more abundant than females". He concluded that adult males have a shorter life span than adult females because the males do not feed: Three adult males examined had empty guts and, following Müller (1894), he agreed that the maxilla and

Table 4.2 Sex ratios (♂:♀) for instars IV-VII of *Cycloleberis*.

	Instar IV	V	VI	VII
sex ratio	0.615	1.113	0.915	0.030
χ^2	14.785	1.017	1.296	339.267
probability	<.001	n.s.	n.s.	<.001
n	260	355	649	382

0.584
χ^2 = 113.380 p <.001

0.980
χ^2 = 0.100 p n.s.

Table 4.3 Burrowing rates of adult *Cycloleberis*. Time (seconds) from commencement of burrowing until disappearance beneath sand surface.

	females	males
$\bar{x}$ time (s)	17.0	24.083
SD	8.87	7.681
n	18	12

t = 2.324, p <.05

fifth limb of these males "are unsuitable for food gathering". This seems unlikely. Adult male *Cycloleberis* evidently feed normally as seen by their full guts when held in the lab. and some of these individuals lived for up to 8.5 months, but not as long as adult females (Table 4.4). Thus the low numbers of final instar male *Cycloleberis* taken during the sampling programme may be attributed to a shorter life span. Increased mobility in search of mates with less time spent in the sand probably results in increased mortality from predation.

Seasonally, sex ratios vary considerably for instars V and VI (Fig. 4.3). There is no regular change in the fifth instar sex ratio but in instar VI, males tend to predominate between June and Sept. - Oct., and females dominate during Feb. - Mar. At other times the sex ratio fluctuates near parity. These seasonal changes in sex ratios probably result from differences in the times at which sexes moult into and out of this instar, thus implying different growth rates for each sex.

SEASONAL POPULATION STRUCTURE

The seasonal instar composition of the population is presented in Fig. 4.4. Here the numbers of each instar 0.1 m^{-2} are plotted against time for the 24-month sampling period. Instars I and II are markedly seasonal in occurrence with very distinct peaks of abundance during summer months. In all subsequent instars peaks of abundance also are apparent, but less distinct and some instars are present in the population for most or all of the year. The frequency of males and females in instar V is similar. Within the sixth instar however, the small yet consistent differences in numerical occurrence of sexes suggests that males enter and leave this instar earlier than do females. This difference in timing accounts for the regular fluctuations of sex ratios (Fig. 4.3) observed for the penultimate instar.

By following peaks of abundance in subsequent instars, the cohort originating in the 1978-79 summer may be followed through successive instars. First instar individuals were most abundant in Dec. - Jan. and passed rapidly into instars II, III and IV by about June. The cohort remained in instar IV for most of the winter but as early as Sept. a few individuals entered instar V. By the second Jan. the entire cohort was in its fifth instar and the moult into instar VI appears to follow closely. It is difficult to follow this cohort reliably beyond instar V because, as growth proceeds, the time required for the entire cohort to pass through an instar increases so that cohorts tend

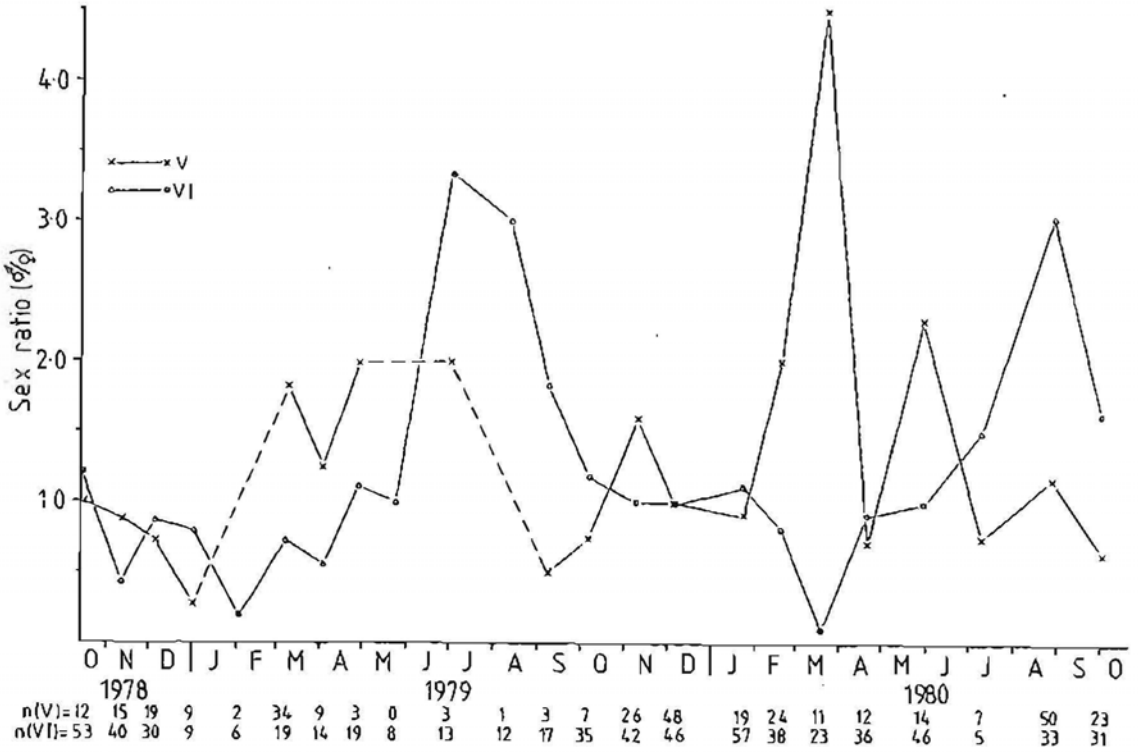

Fig. 4.3. Monthly sex ratios (♂:♀) of *Cycloleberis* instars V and VI. Dotted lines span months in which 0-2 individuals were collected.

to overlap and peaks of abundance become indistinguishable from sample variation. This disappearance of peaks of abundance in later cohorts probably results from differences in individual growth rates, a factor which must be considered in interpreting the last two instar-frequency plots.

Examination of the previous summer's (1977-78) cohort provides a better picture of the life history through instars VI and VII. Here also the moult from fifth to sixth instar seems to occur over the summer months until about Mar. or Apr. Some faster growing males and females of this cohort which entered instar VI early in the summer apparently moult into the final instar late in the same summer as suggested by the decrease in instar VI and increase in instar VII abundance during Feb. - Apr. Remaining individuals of this cohort over-winter in instar VI and complete the final moult during Sept. - Dec. of their second year. Fast-growing individuals appear to constitute up to about half of the cohort and presumably females release juveniles the next

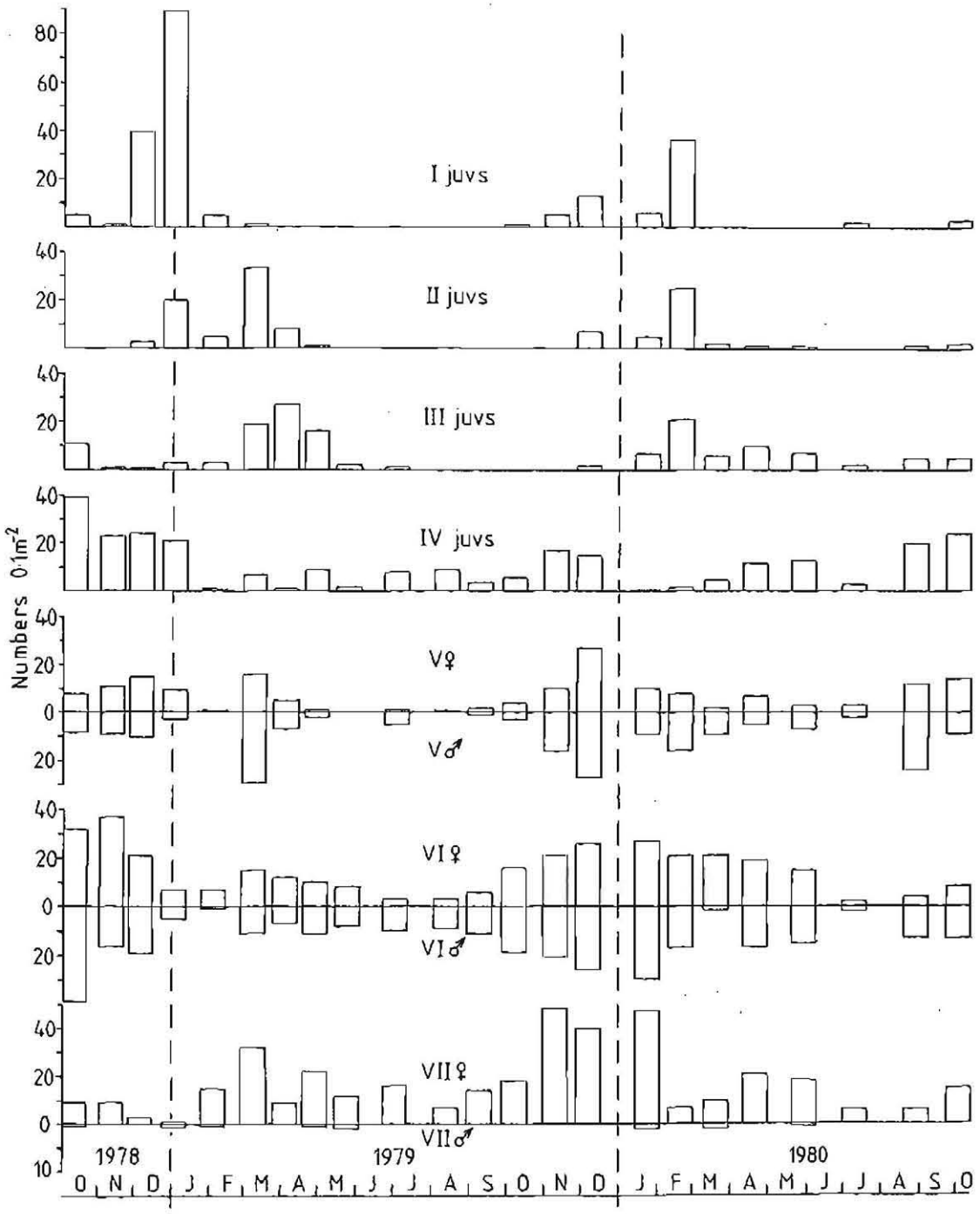

Fig. 4.4 Monthly densities of juvenile, male and female *Cycloleberis* in each instar.

Table 4.4 Occurrence and estimated duration of each instar, and estimated age at end of each instar for male and female *Cycloleberis* from field data. () = estimates using interpolated peaks of abundance.

Instar	Occurrence (months)	Duration (days) first appearance	peaks	last appearance	Estimated age (days)
I	Oct.-Feb.	54	66 (50)	51	50
II	Dec.-Apr.	28	27 (42)	75	78
III	Jan.-May	32	220 (166)	175	135
IV	Mar.-Jan.	149	47 (75)	78	259
V	Sept.-Mar.	40	48 (64)	112	299
VI	all months		88 285		387 584
VII (females)	all months		250 416		637 1000
fast growers		1.8y	2.1y (2.0y)	2.3y	1.8y
slow growers		2.8y	3.1y (3.0y)	3.3y	2.7y

Table 4.5 Life history summary for *Cyclocleberis* (based on the 1978-79 summer cohort).

Event	Fast growers	Slow growers
Release as instar I	Nov. - Dec.	Nov. - Dec.
Moult into instar II	Feb. - Mar.	Feb. - Mar.
Moult into instar III	Mar. - Apr.	Mar. - Apr.
Moult into instar IV	Apr. - May	Apr. - May
Moult into instar V	Sept. - Nov.	Nov. - Dec.
Moult into instar VI	Oct. - Dec.	Dec. - Jan.
Moult into instar VII	Mar. - May	Aug. - Nov.
Produce brood	Aug.	Mar. - May
Release brood	Dec. - Jan.	Aug. - Sept.
Total duration	c.a. 2.0y	c.a. 2.8 y

summer at about two years of age, while the slow growers do not reproduce until later in their third year.

Although the approximate timing of moults from instar to instar is apparent, it is impossible to determine reliably the duration of and age at each instar from these data. Table 4.4 gives months of occurrence and durations of each instar estimated from field data in Fig. 4.4. The duration of each instar has been estimated in three ways: 1, the time from first appearance of instar n individuals until the first appearance of instar n+1 individuals; 2, the time interval between peaks of abundance of instars n and n+1; 3, the interval between the disappearance from the population of instar n and n+1 individuals. Only the second method can be used where individuals of the instar persist throughout the year. These estimates give similar results that seem fairly reliable with one exception. By following peaks of occurrence and the last appearance of instars, the duration of instar III is over-estimated and the duration of instar IV is correspondingly underestimated due to the skewed distribution of the latter.

Despite this error, the estimates of overall life history duration are similar. Estimates obtained by following peaks of abundance seem most reliable. Thus the *Cycloleberis* life history takes about 1.8 - 2.0 years for fast-growing individuals or when favourable conditions permit fast growth in the sixth instar, and about 2.7 - 3.1 years for slower-growers or when the habitat is less favourable (Table 4.5).

Further information on the duration of instars obtained from laboratory growth experiments of 298 individuals kept for various periods (partly depending on individual survival) over 17 months is of limited value. Only 41 of these individuals moulted once and none moulted twice. Thus the entire intermoult period could not be determined for any instar.

REPRODUCTION

Mating in myodocopids is generally thought to occur at night when adults swim into the water column (Elofson, 1941; Kornicker, 1969). Studies by Kornicker (1969) on *Spinacopia sandersi* revealed that during copulation the male attaches two spermatophores just above the female genital opening and he concluded that the eggs probably are fertilized as they leave the oviduct. Apparently a similar sequence of events occurs in *Cycloleberis* as adult

females produced full broods of viable eggs after up to 28 days in isolation. As mentioned above, adult males were taken abundantly only at night and in the plankton. They were accompanied in the plankton by both gravid and non-gravid adult females and individuals of most other instars (see Appendix 1.1). It seems then, that forays into the plankton are not exclusively for mating. In some myodocopids only final instars can swim. For example, in *Philomedes interpunctata*, a benthic species, both adult males and females have elongate swimming setae. After mating the female returns to the benthos and chews them off (Elofson, 1941).

BROOD SIZE AND SEASONALITY

Adult female *Cycloleberis* brood up to 47 eggs ($\bar{x}$ = 37.04, SD = 5.528, n = 200) at once and the mean brood size increases linearly with female size following the relationship Y = -17.159 + 9.543X ($r = 0.772$, $p < .01$). Logically, larger females must have a greater capacity to produce eggs and a larger brood space.

There are negligible differences in the mean brood size during the year (Fig. 4.5). The proportion of adult females brooding however, is quite seasonal (Fig. 4.6), as is the proportion of first instar juveniles in the population. Although differences between seasons are apparent, the overall pattern is similar; few brooding adult females occur during Jan. - Mar. but there is a sharp increase to about half the females brooding in Apr. During May - June there is a decline in the numbers brooding embryos followed by a sudden increase through July - Sept. to 60 - 80% gravid by Sept. - Oct. The abrupt decline to low numbers brooding in Dec. - Jan. corresponds to the period of maximum first instar recruitment (Figs 4.4, 4.6) as they are released by adult females. In 1979 there was only a single release of recruits but in 1980 a second, smaller period of recruitment occurred around July as broods from the Apr. peak were released. Hence, *Cycloleberis* populations may have two recruitment periods annually although the potential for winter recruitment is not invariably realised.

This pattern is seen also in the seasonal frequency of broods at each stage of embryonic development (Fig. 4.7) since all of the eggs in a brood develop nearly synchronously. Stage 1 eggs occur in most broods during Aug. and in Jan. - Feb. broods of stage 5 embryos predominate. The occurrence of stage 1 broods in Apr. - May was similar in the two years, but the percentage

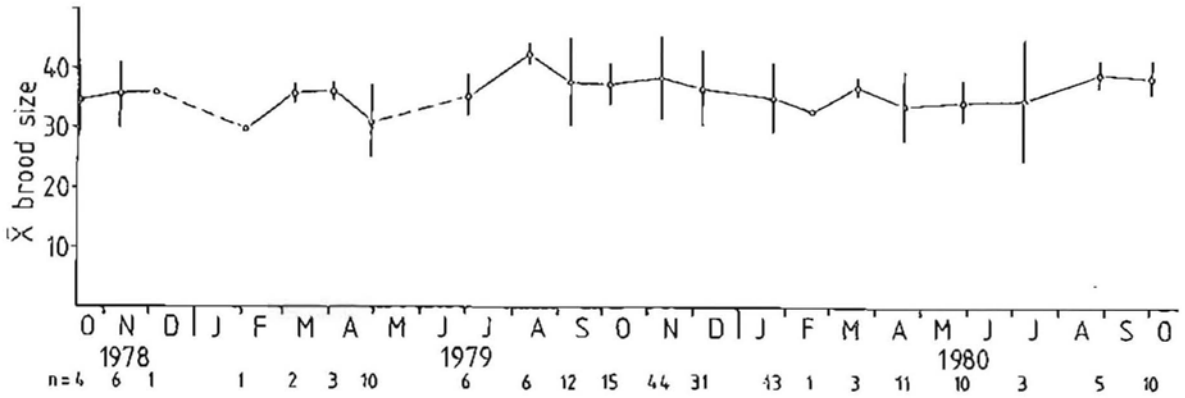

Fig. 4.5 Monthly mean brood size (± SD) of gravid female *Cycloleberis*.

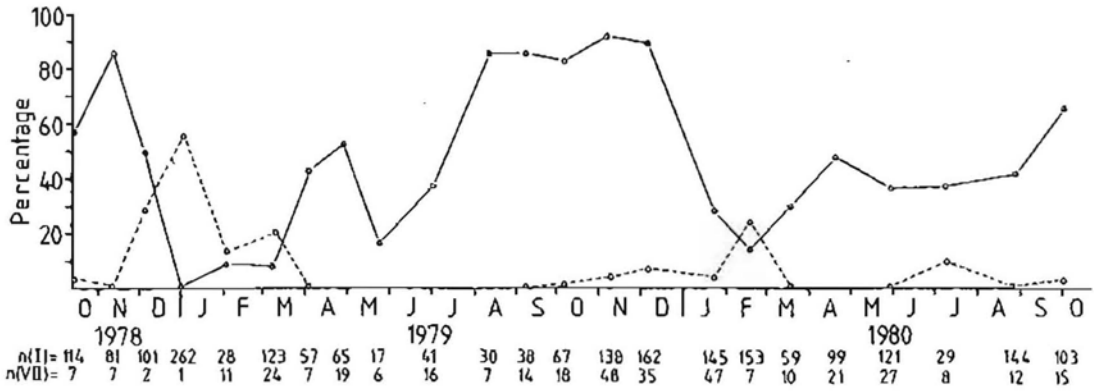

Fig. 4.6 Percentage of instar VII females gravid (solid line) and percentage of first instar individuals (broken line) in the population each month.

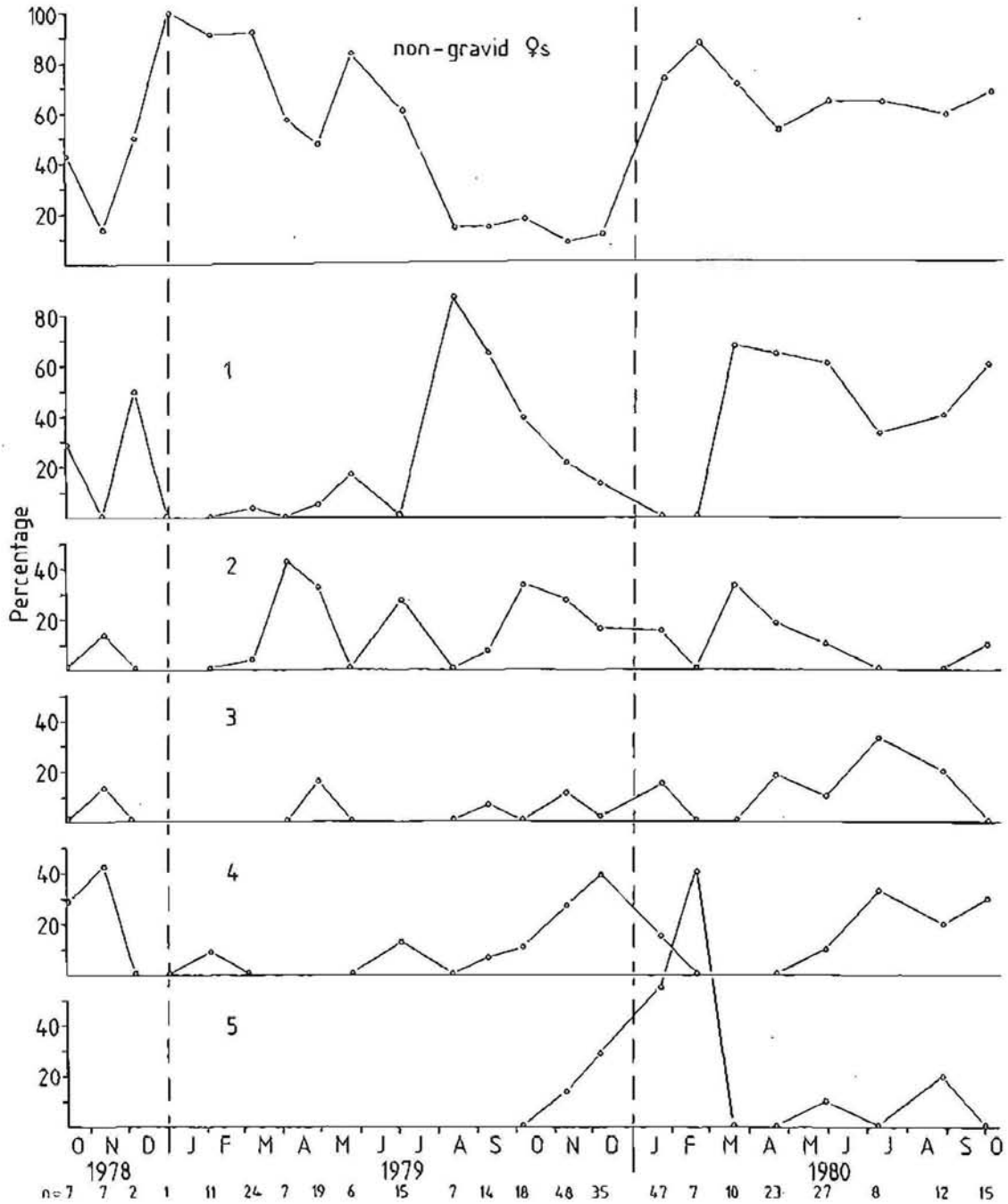

Fig. 4.7 Percent of instar VII females without broods and percent of broods at each stage of development at each month.

Table 4.6 Stages of embryonic development and their sizes (preserved in 70% ethanol) for *Cycloleberis*. Volume was calculated using the ellipsoid formula: $V = 4/3\ r_1 r_2 r_3$ where r_1, r_2 and r_3 are half the length, width and depth of the developing eggs (excluding membranes) respectively.

Stage of development	Morphological characteristics	Length (mm) $\bar{x}$	SD	n	Volume (mm^3) $\bar{x}$	SD	n	significance
1	no trace of an embryo	.841	.076	164	.1692	.0240	29	
								t=3.1631 dfs=75 p<.01
2	embryonic membranes present, somites visible along dorsum	.825	.057	132	.1900	.0335	48	
								t=1.3178 dfs=64 NS
3	carapace formed, small limb buds apparent	.847	.086	54	.1737	.0483	18	
								t=3.8723 dfs=79 p<.001
4	limbs almost fully formed, eyes pigmented and small	.912	.072	118	.2259	.0573	63	
								t=102.6875 dfs=97 p<<.001
5	development appears complete, eyes large, frontal organ visible	.994	.079	69	.2836	.0592	36	
	percent increase 1 → 5.	18.2			67.6			

of females carrying this autumn brood is variable. A few females produced autumn broods during 1979 but none appears to have survived to stage 5. In 1980 by comparison, a large proportion of the adult females produced successful autumn broods that were released in July - Oct.

EMBRYONIC DEVELOPMENT

Five stages of development were recognized in embryos taken from gravid females, although the last one was not distinguished in field samples taken between Oct. 1978 and Oct. 1979. These stages were distinguished by morphological features alone (Table 4.6) and provide no indication of the duration of each stage. Certainly the duration of each stage is not equal. Mean lengths and volumes of each stage included here are seen to increase by 18.2% and 67.6% respectively as development proceeds. Lengths of all stages except stage 5 and presumably volumes also, appear over-estimated in Table 4.7 since the mean lengths of developing eggs measured when alive during the egg development rate experiment (Table 4.7) are generally less than those of preserved material. The living eggs were measured at a greater magnification than were the preserved ones but the observed differences probably result from preservation effects. Despite these differences, the mean length of stage 5 embryos was very similar in preserved and live material. Thus the volume of preserved stage 5 embryos is assumed to represent reliably the living volume of this stage. Using these data *Cycloleberis* embryos increase in volume by 67.6% during development. This is equivalent to an increase in length of 33.2% from early stage 1 to late stage 5. In comparison the increase in length which occurs when the late stage 5 embryo is released to become a first instar juvenile ($\bar{x}$ length = 1.562 mm, SD = 0.028, n = 171) amounts to 57.6% and the overall increase in length from undeveloped egg to first instar is 90.6%.

Differences in mean egg size (length) are apparent from season to season and between years (Table 4.8) although these are not consistent. In 1979 eggs of the autumn brood were larger than those of the spring brood, while there was no significant difference in sizes of eggs from the two broods during 1980. Autumn brood eggs were similar in size both years but spring brood eggs were significantly larger in 1980 than in 1979. No relationship between egg sizes and brood sizes (Fig. 4.5) are apparent but the larger spring brood eggs in 1980 coincides with a lower proportion of instar VII females gravid compared with the previous spring (Fig. 4.6).

Table 4.7 Mean lengths (mm) of developing eggs in living *Cycloleberis*.

	Stage					
	1		2	3	4	5
	very early	total				
$\bar{x}$	0.744	0.773	0.795	0.830	0.935	0.991
SD	0.039	0.034	0.026	0.041	0.054	0.054
n	15	72	33	24	55	45

Table 4.8 Seasonal differences in mean egg (development stage 1) sizes (length, mm) for *Cycloleberis*.

	Season			
	Jan.-May 1979	July-Dec. 1979	Jan.-May 1980	July-Oct. 1980
$\bar{x}$	0.867	0.804	0.893	0.905
SD	0.057	0.054	0.062	0.092
n	6	87	36	27
significance	t=2.627, p<.05		t=0.610, n.s.	
	t=1.002, n.s.			
			t=5.422, p<.001	

Table 4.9 Estimated embryonic development times for *Cycloleberis* populations *in situ*. () = estimates corrected to 15°C, * = estimates from seasonal brood composition data.

Time	Approx. temperature (°C)	$\bar{x}$ appearance	Duration (days) peak	last appearance
1978-79 summer cohort				
Nov.-Jan.	15.0		52	
Jan.-Apr.	15.75			142 (149)
1979-80 summer cohort				
Apr./May-Oct.	11.75	185 (145)		
Nov.-Feb.	16.3		101 (110)	
*Aug.-Feb.	13.98		191 (178)	
1980 winter cohort				
Jan.-May	15.0	128		
Apr.-July	12.5		81 (68)	
*Mar.-Aug.	12.58		162 (136)	

The duration of embryonic development (release of eggs into brood space until liberation of first instar juveniles) was estimated (Table 4.9) by following the peaks of abundance of each embryonic development stage from Fig. 4.7. Estimates were corrected to 15.0°C (in parentheses) assuming an approximately linear relationship between temperature and development rate following Edmondson & Winberg (1971) and Keen (1979). Four of these corrected estimates are remarkably similar and provide a mean embryonic development time of 139.5 days (SD = 9.40).

Laboratory observations on 44 brooding female *Cycloleberis* between 10 Oct. and 28 Dec. 1979 yielded further estimates of development times. In

these experiments it proved impossible to distinguish early developmental stages through the parent's valves. The appearance of eye pigment was the only readily identified developmental event. Further, although all eggs developed during the experiment and some non-gravid females produced full broods, I was unable to rear embryos through to hatching of first instar juveniles. Nonetheless, this experiment, carried out at 15°C, produced some useful estimates.

Five females produced full broods while under observation and their eggs developed to beyond the stage of eye pigmentation. The embryos of another six females proceeded from before eye pigmentation to almost complete development; these embryos appeared more completely developed than any taken in the field. Results are given in Table 4.10. Considering that development did not proceed to completion during this experiment, the total development time must approximate or exceed the maximum estimated duration of 136 days at a mean temperature of 15°C.

Table 4.10 Estimated embryonic development times for *Cycloleberis* held at constant 15°C.

Development stage	No. broods	range	Duration (days) $\bar{x}$	SD
egg release to appearance of eyes	5	57 - 67	63.8	2.28
appearance of eyes to late stage 5	6	30 - 69	43.2	13.8
estimated total development time	minimum	87 days		
	mean	107 days		
	maximum	136 days		

A third means of determining the duration of brood development was available in adult females held individually in running seawater at the E.P.F.S. Here water temperatures fluctuated markedly and visits to check these cultures were at best, monthly. Observed development times and times corrected for monthly mean tank water temperatures are given in Table 4.11. Using the corrected estimates, the longest minimum times observed here range from 135 to 148 days while the lowest maximum times were 148, 181, 199 and >133 to >176. These suggest a development time of around 150-180 days at 15°C.

Comparison of the total observations in Tables 4.9 - 4.11 suggest that the embryonic development time at a mean temperature of 15°C may be more than 5-6 months (160 - 180 days), but there is considerable variation between estimates.

Table 4.11 Estimated embryonic development times for *Cycloleberis* held in running seawater at the Kaikoura laboratory. () = estimates corrected to 15°C.

Incubation period	$\bar{x}$ temperature (°C) min.	max.	no. broods	Duration (days) min.	max.
1979					
4 July/16 Aug.-18 Dec./19 Jan.	13.6	13.7	3	116(106)	198(181)
16 Aug./5 Oct.-18 Dec./19 Jan.	16.5	14.4	1	74(81)	154(148)
1980					
<27 Mar.-28 Aug./3 Oct.	13.4	13.6	2	151(135)	>192(>174)
27 Mar./ 19 Apr.-3 Oct./2 Nov.	13.1	13.7	3	169(148)	218(199)
19 Apr./30 May->2 Nov.	12.9	13.3	1	158(136)	>198(>176)
<30 May-3 Oct./2 Nov.	12.3	12.9	2	128(105)	>155(>133)
<30 May->2 Nov.	12.9		7	158(136)	>158(>136)

BROOD MORTALITY

Observations on the numbers of eggs in broods at different stages of development (Table 4.12) show no brood mortality or losses of eggs during

Table 4.12 Brood size at each stage of embryonic development in *Cycloleberis*.

	Stage of development				
	1	2	3	4	5
Field data					
$\bar{x}$	37.047	35.354	37.790	38.238	37.074
SD	6.219	6.265	5.329	5.093	5.797
n	64	48	19	42	27
Lab. data					
$\bar{x}$	38.9	34.9	34.7	33.6	32.9
SD	2.97	4.03	4.06	3.70	2.04
n	21	19	18	18	7

embryonic development in *Cycloleberis* taken in the field. Apparent egg losses in the lab. (Table 4.12) suggest significant mortality ($r = 5.6387$, $dfs = 80$, $p < .001$). This result is however, disregarded as the egg losses probably are apparent only; as the embryos developed and increased in size they overlay each other rendering some embryos uncountable.

Each adult female *Cycloleberis* appears to produce only one brood of eggs during its life time. I can find no evidence to suggest otherwise and seven females that each released a single brood while in captivity died within one to five months.

GROWTH

As in ostracods generally, growth in *Cycloleberis* is determinate; that is, the number of instars is fixed with no moulting beyond instar VII. Further, this ostracod is mature only in the final instar.

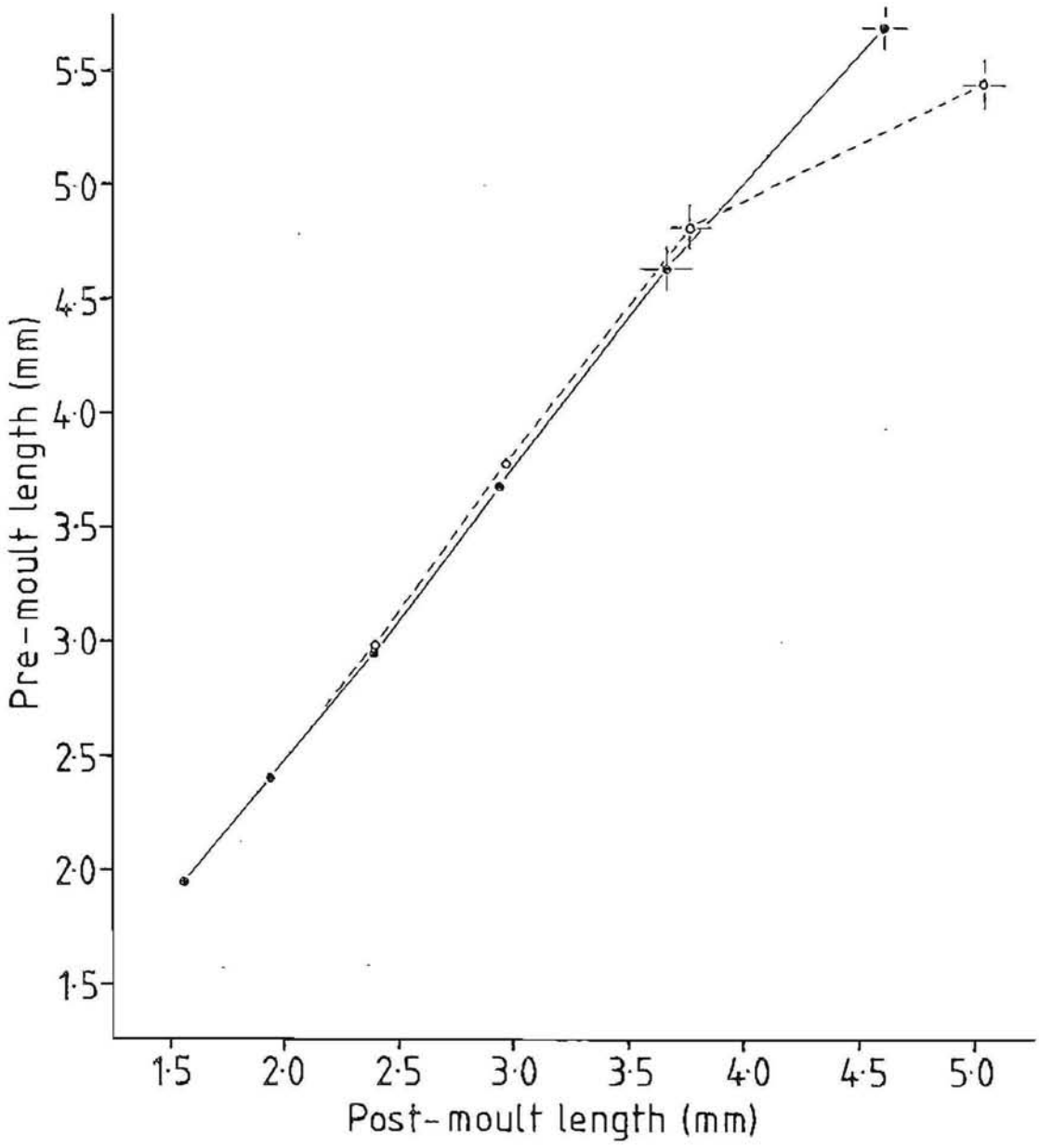

Fig. 4.8 Hiatt diagram for *Cycloleberis*. Solid line, juveniles and females; broken line, males; vertical and horizontal bars, ± lSD (SD <0.1 not shown).

A lot has been written on crustacean growth generally and much of this on the growth of ostracods alone. Many earlier workers explored potential "laws of ostracod growth" (Anderson, 1964; Kesling, 1952; Kesling & Takagi, 1961), in attempts to describe mathematically the size increments at each moult. It is now generally accepted that the relationship between pre-moult size and post-moult size differs between species and within species it may change with the age (instar) of the individual (Kurata, 1962). Hiatt's method of plotting pre-moult size against post-moult size effectively summarises the growth pattern of *Cycloleberis* (Fig. 4.8): Size increments at each moult are proportionally very similar for all but the last moult in both males and females. Males however, grow by proportionately larger increments, again excepting the last moult. The proportionate increment at the final moult is slightly less in females and very much less in males as seen by the inflexions of the respective lines. Such inflexions are usually taken to indicate the onset of sexual maturity when full development of the gonads begins (Kurata, 1962).

Estimated durations of instars presented in Table 4.4 indicate that like most other Crustacea (Hartnoll, in press), the intermoult period of *Cycloleberis* tends to increase with size, but not regularly since growth rates apparently vary with season. Using the estimated ages given in Table 4.4, the growth curve for *Cycloleberis* (Fig. 4.9) indicates that the potential maximum size is not greatly reduced by the terminal moult. This curve further implies that the population is divisable into a faster growing component and a slower growing component by the fourth instar.

VARIATION

Within each instar individuals vary in size (Fig. 4.2) and the range of variation apparently increases with instar number. Calculation of coefficients of variation (CV) for each instar permit more realistic comparisons of within-instar length variation independent of the value of the mean (Sokal & Rohlf, 1969). These are plotted for each instar in Fig. 4.10. Surprisingly the amount of variation does not simply increase with later instars as might be expected. Instead there is an increase in size variation in instars II and III, and also IV in males, followed by a reduction to less variation in final instars.

Changes in instar length variation with instar number apparently are common to all species of ostracods, both myodocopids and podocopids, and to

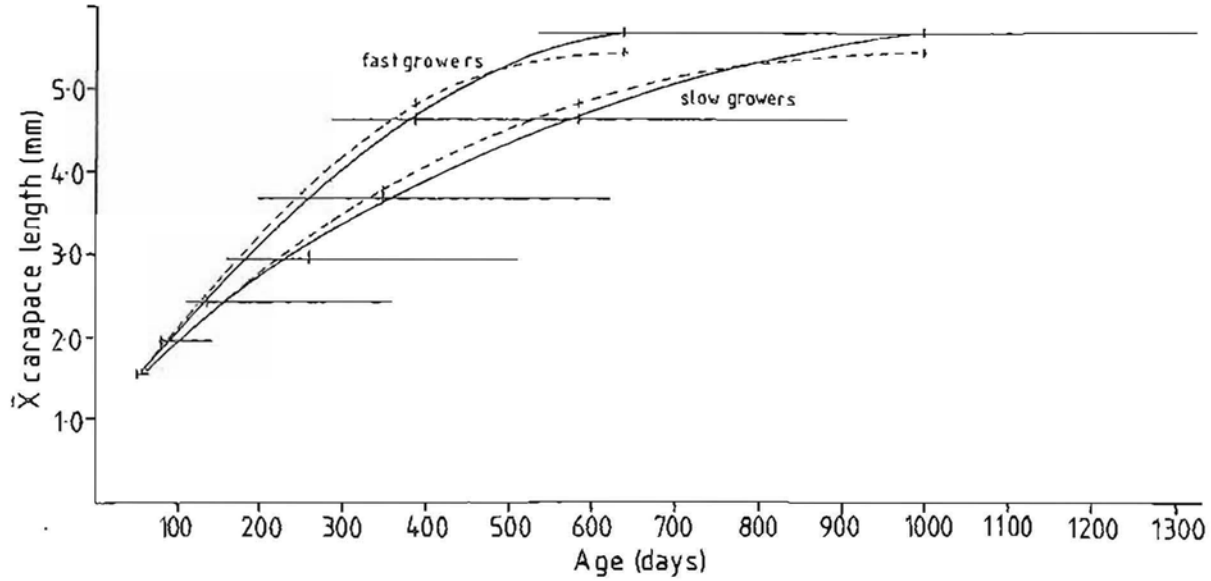

Fig. 4.9 Growth curves (fitted by eye) for fast and slow growing *Cycloleberis* using estimated mean age and duration of each instar from Table 4.4. Solid lines, juveniles and females; broken line, males.

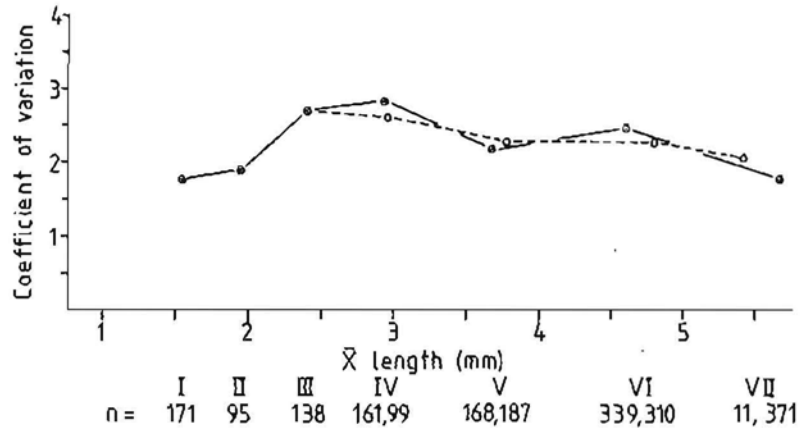

Fig. 4.10 Instar size variation (coefficients of variation) for *Cycloleberis*. Solid line, juveniles and females; broken line, males; vertical bar, ± 1SE (SE <.02 not shown).

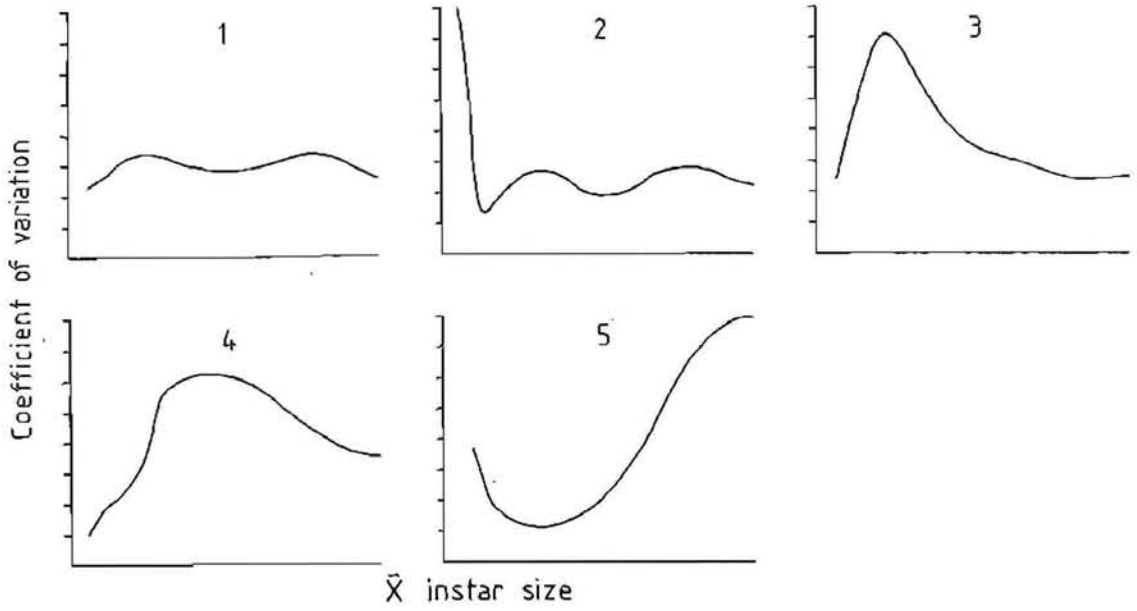

Fig. 4.11 Patterns of instar size variation among ostracods (see text for explanation).

decapods and Cladocera (Hartnoll & Dalley, 1981). Examination of instar length variation plots for 14 species of ostracods for which data are available in the literature* suggests five patterns of instar length variation.

1. Variation independent of instar number. E.g. *Cycloleberis zealandica, Cypridina norvegica, Cypridinopsis vidua* and possibly *Conchoecia lophura* and *Eucypris lutaria* (Fig. 4.11a).

2. High maximum variation in instar I declining to fluctuate at moderate variation from instar II and later instars. E.g. *Cyprideis torosa, Cyprideis baetica* (data incomplete), *Candona neglecta, Cyclocypris laevis* (smaller fluctuations) (Fig. 4.11b).

3. Maximum variation in instar II followed by a rapid decline to low variation in the third and subsequent instars. E.g. *Spinacopia sandersi, Conchoecia aquiseta* (data incomplete) (Fig. 4.11c).

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* Sources of data: *Cyprideis torosa*, Heip, 1976; *C. baetica*, Harten, 1975; *Cypridinopsis vidua*, Kesling, 1951; *Cyprinotus* sp. Kurata, 1962; *Cypricercus fuscatus, C. reticulatus, Cyclocypris laevis, Eucypris lutaria, Candona neglecta*, Heitkamp, 1979. *Spinacopia sandersi*, Kornicker, 1969; *Cyrpidina norvegica*, Skogsberg, 1920. *Conchoecia ametra, C. aquiseta, C. lophura*, Angel, 1979.

4. Low initial variation, high variation in middle instars (III-V) declining to moderate variation in the penultimate and final instars. E.g. *Cyprinotus* sp. (Fig. 4.11d).

5. Moderate variation in instar I declining to low variation in instars II-IV and a steady increase in subsequent instars to a high maximum variation in the final instar. E.g. *Cypricercus fuscatus*, *Cypricercus reticulatus* (data incomplete), *Conchoecia ametra* (data incomplete) and perhaps *Eucypris lutaria* (data incomplete) (Fig. 4.11e).

Several points are immediately obvious from these plots. Firstly, between and within species the amounts of instar length variation vary greatly even when the standard errors are considered. Secondly, the pattern of instar length variation for a species may change gradually when cultured at successively warmer temperatures (*Cyprinotus* sp., Fig. 4.12). Thirdly, the instar length variation pattern for a species is usually very similar to the instar variation patterns for height and for breadth (*Candona neglecta*, Fig. 4.13; see also *Cyclocypris laevis* and *Cypricercus fuscatus* (Heitkamp, 1979)), showing that the instar length variation pattern reflects the pattern of instar variation in volume.

The dispersion of within-instar sizes logically would be expected to increase with instar number and probably in direct proportion to size (instar number). Thus the resulting instar variation curve would be a horizontal line where the within-instar variation increased in direct proportion to instar number. This situation is approximated by the Type 1 pattern exhibited by *Cycloleberis*, *Cypridinopsis vidua* and *Conchoecia lophura* where the CV for each instar lies within ± 1 CV of the mean. Other expected patterns of instar variation with instar number include either a steady increase in CV resulting from the accumulation of successive random fluctuations in moult increments, or a steady decrease in CV due to increasing restraints on moult increment fluctuations. Such patterns however, are not apparent in the species examined. Instead, the patterns of change in instar variation through several units of the coefficient of variation suggest strong discrimination for and against variation of instar size operating variously at different stages in different species.

In the Type 2 variation pattern, the high variation of the first instar is severely reduced after which there tends to be an overall slight increase

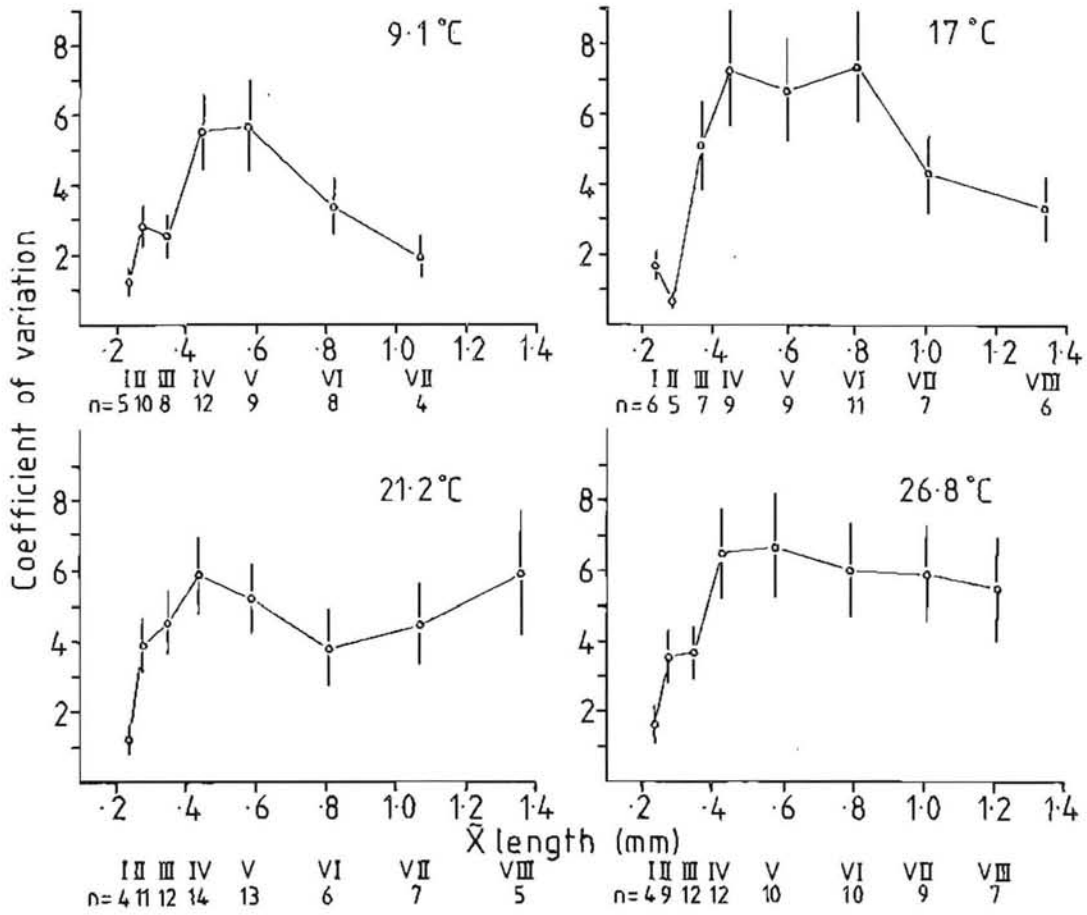

Fig. 4.12 Effect of temperature on the pattern of instar size variation in *Cyprinotus* sp. (data from Kurata, 1962). Vertical bars, 95% confidence limits; arrows, onset of gonad maturation.

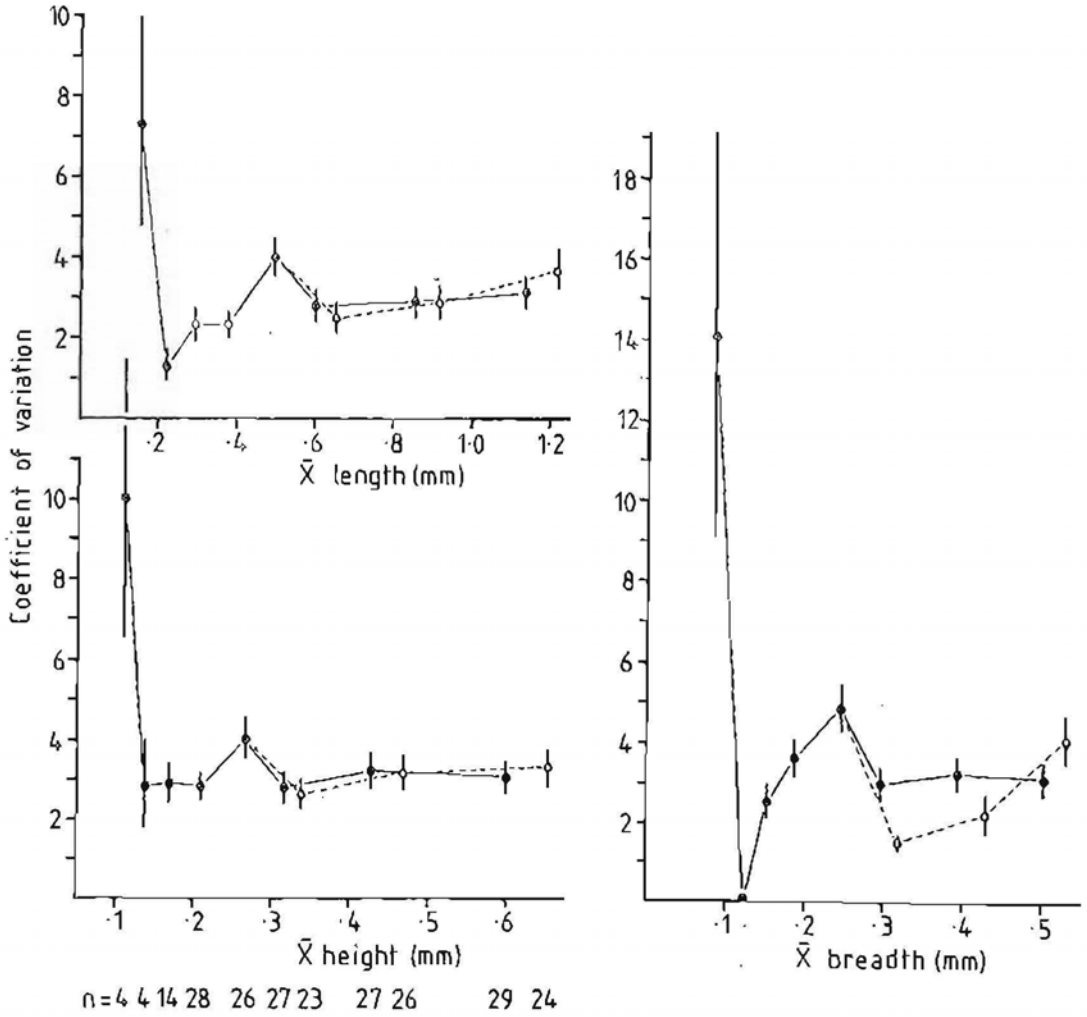

Fig. 4.13 Pattern of instar size variation in length, height and breadth of *Candona neglecta*. Solid lines, juveniles and females; broken lines, males; vertical bars, 95% confidence limits.

in variation to the final instar. The Type 5 pattern is similar in that initial variation is reduced but it differs in that there is no apparent restriction of variation in later instars. Type 3 and 4 variation patterns also are similar to each other and differ principally in the degree and timing of variation constraints. Variation increases from moderate to maximum values in instars 2 - 3 in Type 3 pattern whereas in the Type 4 pattern the variation increase from low initial values to maximum in instars IV - V is less abrupt. Further, the later decline in variation is greater and steeper in the Type 3 pattern.

FECUNDITY AND MORTALITY

As seen in Fig. 4.1 the South Bay *Cyclocypris* population undergoes marked seasonal fluctuations in density. Some understanding of these fluctuations is possible by following the densities of cohorts from instar to instar (Fig. 4.4, Table 4.13). Here cohort A is that originating before the 1978 summer and consisted of instar III - VII individuals only during this study. Cohort B originated in Oct. 1978 - Mar. 1979 as first instar individuals that were followed through to instars VI and VII. Cohort C has its origin in the 1979-80 summer and was followed to instar V - VI. The pattern of changing mortality rates with age, expressed as instar number here, is best specified in the form of a life table (Caughley, 1966). Instar density data from Fig. 4.4 are expanded into instar life tables for cohorts B and C in Table 4.13. The highest mean density of instar n individuals in each cohort was used to calculate the proportion of the cohort surviving from instar n-1 to instar n. These instar life tables form a kl_x series (Caughley, 1966) since the data were obtained directly by following each cohort through its various stages.

Several points arise from these data. First, there is a large difference in the frequency (density) of embryos that gave rise to each cohort. Principally this is attributable to the very large difference in the frequency of parental gravid females (7.714 for cohort B and 44.0 for cohort C) and to a lesser extent, the different mean brood sizes (35.70 for cohort B and 38.227 for C). The reason for such low numbers of cohort B parent females is unknown and Fig. 4.4 shows that any event that may have caused this occurred before the study began. Figure 3.3 shows that the 1979 winter was calmer than the following winter and possibly calmer than most winters. Perhaps these calmer conditions reduced mortality of adults allowing more to produce cohort C embryos. Further, these calmer conditions along with warmer spring water temperatures in 1979 (Fig. 3.4) may have enabled greater food assimilation by cohort C parental females producing the observed 6.6% increase in brood size.

Second, the mortality rate (q_x) between embryos and first instar juveniles is very different between years. Figure 4.6 shows that between 6 Dec. 1979 and 23 Jan. 1980 the frequency of gravid females declined very sharply whereas the frequency of instar I individuals did not increase until after 23 Jan. 1980. Figure 4.4 shows that the frequency of adult females did not decline during this period. These points indicate a very heavy mortality of newly released juveniles between 6 Dec. 1979 and 23 Jan. 1980. Reference to Fig. 3.3, to

Table 4.13 Instar life tables for cohorts B and C of the South Bay *Cyclocleberis* population during 1978-1980. ? = estimate not reliable since data for this instar incomplete; *where a later instar was found at higher frequency then survivorship and mortality between this instar and the last earlier instar at higher frequency is assumed constant and intervening instar frequencies, etc. calculated accordingly; +frequency doubled since adult males inadequately sampled.

Cohort B: $\bar{x}$ gravid ♀s $0.1m^{-2}$ = 7.714, $\bar{x}$ embryos/gravid ♀ = 35.70 $0.1m^{-2}$

Cohort C: $\bar{x}$ gravid ♀s $0.1m^{-2}$ = 44.0, $\bar{x}$ embryos/gravid ♀ = 38.227 $0.1m^{-2}$

	stage	frequency (nos $0.1m^{-2}$)	adjusted frequency*	$1000\ell_x$	$1000d_x$	$1000q_x$
Cohort B						
	embryos	275	275	1000.0	676.4	676.4
	I	89	89	323.6	23.3	71.7
	II	33	82.6	300.4	23.3	77.6
	III	27	76.2	277.1	23.3	84.1
	IV	17	69.8	253.8	23.3	91.4
	V	54	63.4	230.6	23.3	101.0
	VI	57	57	207.3	54.6	26.3
	VII	?21	42+	152.7		
Cohort C						
	embryos	1682	1682	1000.0	978.6	978.6
	I	36	36	21.4	1.5	70.1
	II	25	33.5	19.9	1.5	75.4
	III	21	31	18.4	1.5	81.5
	IV	24	28.5	16.9	1.5	88.8
	V	26	26	15.5	3.0	193.6
	VI	?21	21	12.5		
	VII					

meteorological observations and to my own records show that severe storm waves pounded the shores in South Bay between 2 - 10 Jan. 1980. This catastrophic mortality of juveniles almost certainly was caused by the storm.

Third, although it is not possible to determine the true mortality rates for successive instars between the first and sixth in cohort B, the overall mortality rate here (q_x = 359.4, d_x = 116.3) is quite high. In cohort C the overall mortality rate between the first and fifth instars is similarly high (q_x = 275.7, d_x = 5.9) and, assuming similar mortality between instars V and VI, then the mortality rates for both cohorts probably are very similar, even though the density of cohort B individuals is twice that of cohort C individuals.

The occurrence of a second lesser recruitment of instar I individuals in winter (July) of some years may in part be associated with the summer (Jan.) recruitment failure and in part to other factors. When a second period of recruitment did occur, the preceeding summer mean water temperatures reached 14.0°C one month earlier and remained at or above 14.0°C for one month longer than the previous summer (Fig. 3.4). These conditions then, may have enabled a few cohort B sixth instar females to undergo their final moult during the 1977-80 summer and to release offspring the following winter.

DISCUSSION

The pattern of seasonal density changes observed for *Cycloleberis* is typical of species with a single, brief period of recruitment annually. Data on *Parasterope pollex*, the one other benthic myodocopid studied seasonally, show a similar pattern of density changes with a spring peak abundance of 12,000 m^{-2} resulting from the annual release of juveniles (Hulings, 1969). Maximum densities of *Cycloleberis*, a considerably larger species ($\bar{x}$ adult female length 5.68 mm c.f. 1.56 mm), were only 3,500 m^{-2}.

Examination of annual population densities alone reveals little, whereas the yearly change in instar abundance can show periods of recruitment, instar longevity, mortality patterns and generation time. This approach was largely ignored by Hulings (1969) in his study of *Parasterope* even though instars were distinguishable by size. *Cycloleberis* passes through a total of seven instars readily separated by size and with no overlap between instars. In the past most attempts to distinguish instars have been morphological, largely because few specimens were available. Other workers endeavoured to predict

the number of instars and their sizes by applying Brooks' Principle (Brooks, 1886), which stated that the length of instar n+1 equalled 1.25 times the length of instar n (e.g. Skogsberg, 1920; Poulsen, 1965). This approach is now largely discredited and, in the absence of a large series for length measurements, instars are best separated using Kornicker's (1969) morphological key.

As a consequence of this problem, the number of instars in families of the myodocopids is imperfectly known. Within the three suborders of Myodocopida, I can find no mention of the number of instars in species of the suborder Cladocopina. There are generally seven instars in species of the Halocypridina (Angel, 1979) although eight were reported by Tseng (1975) in his study of *Euconchoecia elongata*. Families of the Myodocopina have five to seven instars: five in the Sarsiellidae (n = 3 species), six or seven in the Cypridinidae (n = 5 species) (Kornicker, 1969), six in the Philomedinidae (n = 2 species) (Elofson, 1941; Baker, 1978), and seven in the Cylindroleberididae (n = 2 species) (Hulings, 1969; present study). The number of instars for species of the Rutidermatidae is unknown.

The significantly larger size of instar IV to VI males seen here in *Cycloleberis* has not been reported for other species, again probably because of the scarcity of specimens. This size disparity occurs in at least one other species of *Cycloleberis*; limited data available show that sixth instar males of *Cycloleberis christiei* are longer ($\bar{x}$ = 4.46 mm, SD = 0.152, n = 5) than instar VI females ($\bar{x}$ = 3.98 mm, SD = 0.152, n = 5) (Kornicker & Maddocks, 1977). Unlike *C. zealandica* however, adult males of *C. christiei* are longer than adult females ($\bar{x}$ = 5.5 mm, SD = 0, n = 2 c.f. $\bar{x}$ = 5.06, SD = 0.26, n = 7) but the more elongate valve shape is common to males of both species. A cursory survey of the few length measurements available for adult males and females in Poulsen (1962, 1965) and Kornicker (1975) (Table 4.14) reveals that within the Cypridinidae and the Sarsiellidae, females tend to be larger than males (n = 24 and 11 respectively), there is a tendency for larger males in the Philomedidae (n = 8), and within the Cylindroleberididae and the Rutidermatidae species with males larger than females are as frequent as species with males smaller than females (n = 15 and 4 respectively). Females of the halocyprids are usually larger than males (26 of 28 species (Angel, 1979)). Several points suggest that adult sexual size disparity in favour of females may be advantageous to a species: The smaller size of adult males conceivably lowers the energy requirements of this sex in the penultimate and final instars,

Table 4.14 Occurrence of sexual length dimorphism in adult myodocopid ostracods. Data from Poulsen (1962, 1965), Kornicker (1975), Angel (1979).

	No. species with relative adult length		
	♂>♀	♂<♀	♂ c.a.=♀
Myodocopina			
Cypridinidae	3	21	0
Philomedidae	5	3	2
Rutidermatidae	2	2	0
Sarsiellidae	0	12	0
Cylindroleberididae	7	7	1
Halocypridina	2	26	0

thus reducing competition with females of these instars. Reduced competition could shorten the duration of the female penultimate instar. Thus for a given instar duration, both sexes may mature simultaneously, but the females may be larger enabling them to produce and to carry more eggs. However, the minimum male size and the sexual size disparity of each species must be limited by the males' ability to search for mates and to copulate successfully. Male planktonic halocyprids range from 59.8% to 102.1% of the female size with 25 of the 28 species examined having males larger than 85% of the female size (from Angel, 1979). It is interesting that in the two species of halocyprids where adult males are larger than adult females, the size disparity is no more than 2% of the female size. In the Myodocopina however, adult males may be up to 135.4% of the female length and males lengths in excess of 110% of female length are not uncommon. Rarely are adult males less than 80% of the female

length.

The age structure of the South Bay population of *Cycloleberis* varies seasonally as a consequence of the discrete periods of recruitment and the relatively brief durations of instars I - III. From year to year however, the seasonal age structure varies following the success or failure of the July - Sept. (winter) recruitment. This difference is apparent in the presence of early instars since, by the fourth instar, this cohort appears to merge with the subsequent summer cohort. Further, the proportions of fast and slow growers in the sixth and seventh instars, and the prevailing environmental conditions may alter the seasonal frequency of these instars between years. Thus although there are discrete periods of recruitment to this population, the population density and its seasonal structure varies from year to year in response to environmental factors.

Year to year differences in crustacean population densities and structures, especially harpacticoid copepods, have received considerable attention in recent years (e.g. Harris, 1972; Croker, 1977; Dexter, 1979; Croker & Hatfield, 1980; Feller, 1980), and the inconstancy of these parameters is considered normal for many species. An important effect which contributes to this variation is the irregular occurrence of an additional period of recruitment in some years. This occurred in the *Cycloleberis* population during the 1980 winter. In his study of the intertidal, sand-dwelling harpacticoid *Huntemannia jadensis*, Feller (1980) observed a second annual period of recruitment in only one of three populations studied simultaneously. The second recruitment occurred in winter and, although the density of nauplii produced exceeded the number resulting from the previous normal spring recruitment, the second recruitment individuals did not survive to maturity (Feller, 1980). Further, it appears that after this winter breeding activity, the usual spring recruitment was delayed relative to the previous spring breeding (Feller, 1980, fig. 6a). Even though the *Cycloleberis* population was not monitored through the period of usual summer recruitment following the winter recruitments, evidence suggests that this subsequent summer breeding would have been "normal" (Figs 4.4, 4.7).

Semi-quantitative data on seasonal population structures, and life history details are available for three myodocopid ostracods. There was a single discrete period (c.a. one month) of recruitment annually in *Parasterope pollex* with a consequent regular seasonal pattern to the population structure

(Hulings, 1969). Instars I - III were quite seasonal in occurrence (July - Sept.) whereas all subsequent instars, while apparently exhibiting some seasonality, were present throughout the year. Interpretation of Huling's (1969) fig. 4 is difficult but *Parasterope* appears to mature and reproduce within one year. *Philomedes globosus*, like *Cycloleberis*, is a longer-lived species. Elofson (1941) calculated from laboratory data that it took 2.75 - 3 years for *Philomedes* to mature and that adult females may live for up to four years. My interpretation of his fig. 46, a semi-quantitative summary of seasonal instar abundance, is that *Philomedes* attains maturity after about two years and females produce broods late in their third summer. These are incubated for eight months and juveniles are released in early spring when the parent female is about three years old. By comparison, the life span of the halocyprid *Euconchoecia elongata* is about 56 days and breeding is continuous (Tseng, 1975).

Euphilomedes producta apparently takes about two years from first instar juvenile until maturity (sixth instar) (Baker, 1978). However, since Baker's (1978) collections contained only instars IV - VI, the reliability of his estimate is uncertain. Ovigerous female *Euphilomedes* were found throughout the year and, without examining seasonal changes in the state of development of embryos, Baker (1978) concluded that reproduction appeared to occur year round. In contradiction, his fig. 1 suggests two peaks of adult females and of ovigerous females per year, and his fig. 2 shows a definite seasonality of instars IV and V. These points suggest that the population consisted of two cohorts originating from two discrete periods of recruitment annually.

Cycloleberis zealandica appears to breed once only; the abundance of sixth instar females during an annual cycle is very similar to that of the total adult female population during that period, and gravid females with unextruded eggs were not seen. This latter criterion was taken to indicate that adult females of *Philomedes globosus* and *Euphilomedes producta* may produce two broods of eggs (Elofson, 1941; Baker, 1978). In *Parasterope pollex*, the halocyprid *Euconchoecia elongata*, and probably in *Cycloleberis* also, females die soon after releasing their single brood (Hulings, 1969; Tseng, 1975).

As in most groups of brooding Crustacea, the brood size of myodocopids is variable (Table 4.15) and differences in brood size with taxon are apparent. Brood size is correlated with adult female size within species, within families (Kornicker, 1975 figs. 25 - 28) and between families of the

Table 4.15 Mean maximum brood sizes for families of the Myodocopina. Data from Kornicker (1975) table 18 and Poulsen (1962).

	mean max. no. embryos	SD	n	adult ♀ size range (mm)
Cypridinidae	23.66	17.66	29	1.65 - 34.00
Cypridinidae excl. *G. muelleri* & *M. castanea*	19.48	8.46	27	1.65 - 4.65
Philomedidae	14.45	8.19	29	1.07 - 4.35
Cylindroleberididae	12.66	4.74	41	1.14 - 3.55
incl. *C. zealandica*	13.24	6.00	42	1.14 - 5.68
C. zealandica	37.04	5.53	200	5.68 (mean)
Sarsiellidae	6.87	3.30	30	0.62 - 2.68
Rutidermatidae	4.00	0	6	1.25 - 1.63

Myodocopina (Table 4.15). Within the myodocopid ostracods generally however, *Cycloleberis* has a large adult size and a large brood size. Kornicker (1975) noted that pelagic species such as *Gigantocypis muelleri* and *Macrocypridina castanea* generally produce larger broods (up to 85 and 70 eggs respectively) than benthic species and, when the mean brood size is recalculated for the Cypridinidae excluding these species (Table 4.15) *Cycloleberis* is seen to be even more unusual among benthic myodocopids. Three points however, reveal that this large brood size is not entirely unexpected in *Cycloleberis*: (i) The general correlation between body size and brood size observed for the Malacostraca (Jensen, 1958; Nelson, 1980; Van Dolah & Bird, 1980) appears true also for myodocopid ostracods when Kornicker's (1975, figs. 25 - 28) analyses are considered. (ii) *Cycloleberis* is large among myodocopids. (iii) An obvious means of balancing high juvenile mortality in semelparous species is

to increase the brood size (Stearns, 1976).

Very little information is available on egg sizes of myodocopids. Elofson (1941) reported that *Philomedes globosus* eggs were 0.49 - 0.56 mm long, undeveloped *Euphilomedes producta* eggs averaged 0.28 mm (Baker, 1978), eggs of *Parasterope pollex* measured between 0.20 and 0.30 mm (Bowman & Kornicker, 1967), and developing embryos of *Euconchoecia elongata* range from 0.17 to 0.20 mm in diameter (Tseng, 1975). Compared with these, the undeveloped eggs of *Cycloleberis* (0.841 mm long, Table 4.6) are large. With such wide ranges of egg sizes, brood sizes and adult female sizes, examination of these parameters for species of myodocopids promises interesting results.

The increase in embryo length (18.2%) and volume (67.6%) during development observed in *Cycloleberis* was not unexpected. Similar increases in embryo size with development probably occur in other ostracods since the eggs of aquatic invertebrates generally increase their volume significantly during ontogeny by slow osmotic uptake of water (Davis, 1968). The increase in volume during development of decapod embryos ranged between 65 - 175% ($\bar{x}$ = 116%, n = 19 species) (Wear, 1974). Embryo volumes increase by about 220% on average ($\bar{x}$ = 218%, range 193 - 240%, n = 5 species) in the Amphipoda (Bregazzi, 1973; Williams, 1978; Moore, 1981). In comparison the 67.6% volume increase observed for *Cycloleberis* embryos was rather low.

My attempts to determine the duration of embryonic development for *Cycloleberis* were not entirely successful because brooding females did not survive to release offspring in the lab. and because individuals held in flowing seawater at Kaikoura could be examined at monthly intervals only. Despite this the number of broods followed provided a reasonable estimate of the time involved (Tables 4.9 - 4.11). Thus development of *Cycloleberis* embryos through to hatching takes 160 - 180 days at 15°C. In nature the development time is similar (c.a. 190 days) since, although eggs of the principal summer brood are produced in Aug. when water temperatures are lowest, temperatures remain well above 15°C at least half of the incubation period.

Elofson (1941) reported an embryonic development time of eight months for *Philomedes globosus* in Skagerak where his reported water temperature range was 5.18 - 7.03°C. By assuming an overall mean temperature of 6.0°C here, this time corrected to 15°C (following Edmondson & Winberg, 1971 &

Keen, 1979) is about 96 days or 3.2 months. This compares more favourably with the estimated development time of *Cycloleberis* when egg sizes of the two species are compared. In Crustacea generally the duration of embryonic development increases in direct proportion to the egg size (Steele & Steele, 1975c), and thus, the development time of the smaller (0.49 - 0.56 mm long) *Philomedes* egg should be considerably less than that of the larger (0.841 mm long) eggs of *Cycloleberis*. Fig. 4.14 presents the relationship between embryonic development time (standardized to 10°C) and egg size (= the smaller extreme of a range where given) for four myodocopids. Points for three of these species almost form a straight line whereas that for *Euphilomedes producta* lies well above this line. Baker (1978) supposedly calculated the duration of embryonic development of *Euphilomedes* as 158 days by "extrapolating from the work of Elofson (1941) on *Philomedes globosa* and work of Van Dolah *et al.*(1975)", but makes no mention of temperature. Further, it is difficult to understand how he arrived at this estimate; he seems to have applied Elofson's (1941) estimates for *Philomedes* development at about 6°C to Van Dolah *et al.*'s (1975) regression of egg development time against temperature for two genera of amphipods and ignored the effect of egg size. Careful examination of Baker's (1978) fig. 1 shows two peaks in abundance of ovigerous females, each spanning about 3.5 months (105 days). Reference to Baker (1975, table 4) reveals a mean temperature of 14.04°C in his study area. Thus I have taken the development time of this ostracod as 147 days at 10°C, possibly still an over-estimate when compared with the other three species.

When these four points are plotted on Steele & Steele's (1975c) fig. 2, they lie just above the encircled points for the Decapoda. Hence it seems that for a given egg size, the development rate of myodocopid ostracod eggs is slightly slower than that of decapod eggs.

Brood mortality, or the loss of developing embryos, is common among peracarids but it does not occur in *Cycloleberis* (Table 4.12). No data are available on brood sizes at different stages of development for other myodocopids. Brood mortalities in peracarids are often 20 - 30% and occasionally more than 50%, but in some species, especially Cumacea, such mortality may be insignificant (Moore, 1981). Within the Decapoda also, losses of developing eggs are common and frequently up to about 15% are lost (Jones, 1978). Most of these animals are iteroparous however, so that losses of eggs from a brood may be compensated in subsequent broods. For semelparous

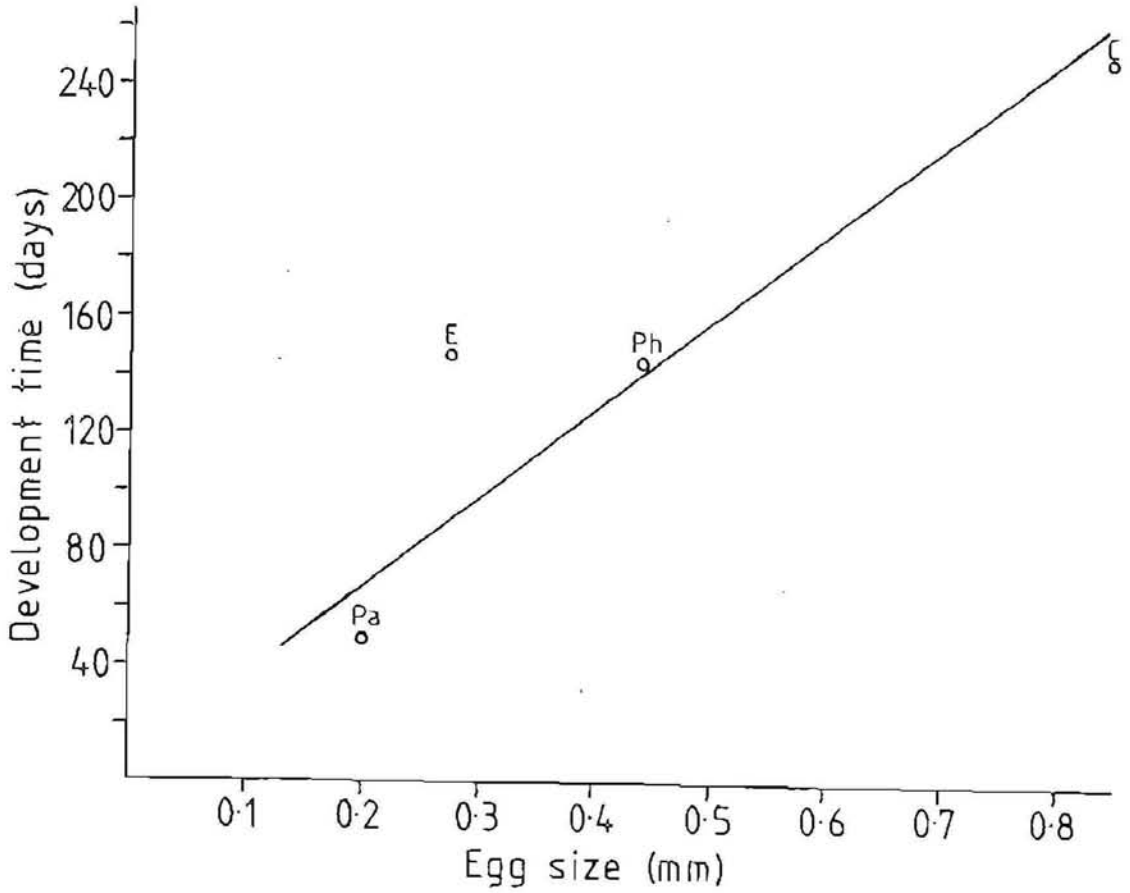

Fig. 4.14 Relationship between egg length and duration of development at 10°C for myodocopid ostracods (line fitted by eye). Pa, *Parasterope pollex*; Ph, *Philomedes globosus*; E, *Euphilomedes producta*; C, *Cycloleberis zealandica*.

species such as *Cycloleberis*, especially when the life history is long, it is important that pre-hatch losses are minimal.

Although growth in ostracods generally is considered determinate, the question of post-adult moulting in some myodocopids remains unanswered. Post-adult moulting does not occur in *Cycloleberis*. Kornicker (1975) reviewed evidence on this question and concluded that if it does occur, post-adult moulting is rare. However the principal arguments advanced for post-adult moulting, namely adults of a few species that fall into two, or possibly three size groups, remain unresolved. Poulsen (1962) concluded that adult female *Gigantocypris agassizi* occurred in three size (length) groups: 23 - 27 mm, n = 13; 30 - 32 mm, n = 5; and 34 mm, n = 1. Females

of the penultimate instar ranged between 16 and 22 mm long (n = 9). Similarly for *G. muelleri*, Poulsen (1962) considered that adult females fell into two size groups: 15 - 17 mm (n = 20) and 19 - 20 mm (n = 2) while penultimate instar females were 12 - 14 mm long (n = 5). Kornicker (1975) attempted to resolve this problem by comparing the variances in lengths of penultimate females with lengths of the combined adult females for each species using the variance ratio (F) test. The use of variances for comparing dispersion or variation of populations is inappropriate however, because variances are dependent upon the magnitude of their means (Sokal & Rohlf, 1969). Further, in applying this test Kornicker (1975) concluded that although the data were inconclusive, *G. agassizi* may undergo post-adult moulting because "adult females of *G. agassizi* almost had a significantly different dispersion at the 0.1 level than juvenile females". In general statistical procedure for 0.05 probability level is adopted for the acceptance or rejection of a null hypothesis (Sokal & Rohlf, 1969).

The coefficient of variation (CV) was developed for comparing population variations independent of their means. Using Poulsen's (1962) data, the CV for the combined mature females (CV = 12.352, SE = 2.004, n = 19) is less than that for the sixth instar females (CV = 13.034, SE = 3.072, n = 9). The variation for combined adult females of *G. muelleri* (CV = 7.669, SE = 1.156, n = 22) is slightly higher than that for penultimate instar females (CV = 6.539, SE = 2.068, n = 5). On the basis of within-instar size variation then, it seems that there is no evidence to suggest post-adult moulting in these two species.

More recently Baker (1978) reported the presence of more than one size class within adult males and females of *Euphilomedes producta*, indicating the occurrence of post-adult moulting in both sexes. For each sex, comparison of length dispersion within fifth instar and within adult individuals using the t-distribution revealed highly significant ($p < 0.001$) dispersion within adults but dispersion within instar V individuals was not significant. As far as I am aware, there is no commonly used method of comparing sample dispersions using the t-distribution. With the absence of data on mean lengths, standard deviations, etc. for instars of this species (Baker, 1975, 1978), there is no evidence for it undergoing post-adult moults.

Just why changes in the amounts of within-instar length variation should occur between successive instars is open to speculation. Data on instar

mortalities and instar size variations could show whether size variation is restricted by death of individuals at extremes of the size range or by compensations in their subsequent moults. Further, an understanding of life histories may permit some correlation between life history patterns and instar size variation patterns. In most of the above examples there is a reduction in variation between the penultimate and final instars or the relative increase in variation with the last moult is less than the increase with the previous moult. This is not unexpected since constraints on the reproductive phase of a life history are likely to be more severe than for other instars.

Data on egg and embryo sizes would be especially interesting for species exhibiting Type 2 and Type 5 variation patterns. The large size variation of instar I individuals of Type 2 species suggests an equivalent variation in egg sizes but there are no available data on egg size variation. This variation is markedly reduced in instar II probably by intrinsic limitation of moult increment to impose size conformity or by mortality of individuals at either one or both extremes of the size range. A similar mechanism probably operates in species exhibiting the Type 5 pattern, although the degree of variation of first instar size, and conceivably of egg size, is not so great.

It is notable that all species exhibiting Types 1 - 3 variation patterns are bisexual (except *Cypridinopsis vidua*) and their coefficients of variation (CV) for adult instars lie between 2.0 and about 5. Species with Type 5 instar length variation tend to have adult CV values considerably greater than 5. The three pododocopids with this variation pattern are parthenogenetic with males unknown (*Cypricercus fuscatus* and *Eucypris lutaria*) or, although males are known, they were not present in the parthenogenetically reproducing population studied (Heitkamp, 1979).

Species of *Cyprinotus* are known to reproduce both parthenogenetically and sexually, and Kurata (1962) observed that his *Cyprinotus* sp. "undergoes a parthenogenesis during, at least, the warmer months". It is possible that the effect of increased temperature on instar length variation pattern may in part be due to a change from predominantly sexual reproduction with its inherent size variation constraints to predominantly parthenogenetic reproduction allowing greater instar size variation (Fig. 4.12). Thus it appears that sexual reproduction imposes limitations on adult instar size variation

whereas parthenogenetically reproducing adult populations are relatively free from such constraints. This observation contradicts the generally accepted ideas that sexually reproducing species are more variable as a result of genetic recombination, whereas parthenogenetic species have less genetic variation and consequently exhibit less morphological variation.

Studies on the copulatory apparatus and copulatory behaviour of ostracods (McGregor & Kesling, 1969) suggest that the mechanics of sperm transfer may exert strong selection against size variation in adult ostracods. Numerous workers (see McGregor & Kesling, 1969: 222-225) have emphasized the extremely complex anatomy of the male ostracod copulatory apparatus and carapace shape appears directly related to the accommodation of the sex organs in many species, especially pododocopids (McGregor & Kesling, 1969). It seems reasonable to infer from this then, that within many species carapace size bears a direct relationship to sex organ size. Further, when in copula the male carapace gapes to overlap the female carapace (except in some ventral-ventral mating species), and a variety of appendages and spines is used to grasp the female and to hold her valves apart. Even then the male and female genitalia are separated by a considerable distance in most species. This distance may be critical for successful mating however, since mating further requires a series of intricate steps: 'paired "male muscles"... contract to bring the hemipenes downward and out of the carapace. The hemipenes then are rotated as one unit through 180 degrees, swing forward between the valves of the female, un-fold in erection, and the glans inserted into the paired vaginae' (McGregor & Kesling, 1969: 230). The complete copulation is very brief taking about 4 s in *Physocypria*, about 15 s in *Candona fabaeformis* and 10 - 25 s in *Candona* spp. Thus, in view of the relationship between carapace size and size of the sex organs, the critical positioning of male and female, the several steps involved in actual sperm transfer and the brief duration of copulation, any intraspecific variation of adult size would appear to render successful copulation more difficult. Consequently selection favouring minimal adult size variation seems advantageous. To examine this problem further it would be interesting to compare instar size variation in sexually reproducing and parthenogenetically reproducing populations of the same species, such as *Cypricercus reticulatus*.

In addition to limitation of variation by the mechanical restraints of copulation, sexual reproduction results in new variations not removed by natural selection becoming widespread in panmictic populations through

syngamy and recombination as the population moves towards genetic equilibrium. Further, the tendency for such populations to show a strong heterozygote dominance further reduces the phenotypic variation of panmictic populations at genetic equilibrium. Similar variations arising in parthenogenetically reproducing populations are not shared but many subdivide the population into phenotypically distinct clones. Thus phenotypic diversity at any one time may be greater in parthenogenetic populations than in sexually reproducing populations.

The initial increase in size variation followed by some limitation of variation seen in Type 3 and 4 patterns suggests that some individuals of each instar initially grow larger while others do not, either through intrinsic or extrinsic factors. Restraint of size variation occurs as maturity is approached by individuals with extreme sizes either dying or conforming by increment adjustments at moults. Recently Hartnoll & Dalley (1981) followed the growth of 54 individual shrimps, *Palaemon elegans*, through instars 1 - 17. The pattern of length variation (CV) was initially low (c.a. 1), increased steadily to five or six by the fifth instar and then declined appreciably in the sixth and seventh instars, the last larval and first post-larval instars respectively. Thereafter it increased to 13.5 - 14.8 in the fourteenth or fifteenth instar and a small decrease occurred in each of the following instars. Thus the decreases in CV at the end of the larval phase and in the final few instars of the experiment occurred via a negative feedback mechanism (Hartnoll & Dalley, 1981) which adjusted individual increments at these moults to ensure that individuals conformed to the optimal size.

Evidence for fast-growing and slow-growing individuals in instars VI and VII comes from the presence of two peaks annually of instar VII females (Fig. 4.4) compared with one annual peak of sixth instar females, the irregular occurrence of a second period of recruitment annually (Fig. 4.7), and the wide range of estimated instar durations (Fig. 4.9). It is unlikely that fast- and slow-growers exist as such, but rather that a range of genetically determined characteristics provides the potential for a variety of growth rates, and the timing of life history events relative to water temperature, food availability and other seasonal phenomena may divide a cohort into fast- and slow-growing components. Apparently the reproductive success of each component of a cohort varies from year to year in response to differences in the seasonal environment. Some insurance against failure

of a breeding or a recruitment is provided by such a tactic. This was seen in the South Bay *Cycloleberis* population where, in the 1978-79 summer, recruitment (cohort B) was relatively high but eggs produced in the following autumn failed to produce any appreciable early spring recruitment. After the next summer when recruitment (cohort C) was low however, several broods completed development and some recruitment did occur. Thus, *Cycloleberis* has minimized the inherent risks of semelparity in a long-lived species by division of each cohort into early and late breeders through differences in growth rates.

A similar situation occurs in the pododocopid *Cyprideis torosa* where the single annual cohort becomes divided in two (Heip, 1976). Juveniles produced in early summer mature in autumn and carry eggs that will give rise to the early summer juveniles over winter. Juveniles produced later in the summer overwinter as late instars to mature and produce eggs in spring. Thus the long period of recruitment and the lack of development during winter because of low temperatures causes the split in *Cyprideis* cohorts.

Cohort splitting is known for one other crustacean, the terrestrial isopod *Philoscia muscorum* (Sutherland *et al.*, 1976), in which females of each cohort, and possibly males also, split into fast and slow growing groups at about maturity when ten months old. Fast-growers bred when one year old whereas slow-growers survived to breed in the following summer at two years of age (Sutherland *et al.*, 1976). Thus cohort splitting was considered to be the principal phenomenon underlying the outstanding population stability (density and size structure) of the isopod (Sutherland *et al.*, 1976) and it is probably an important feature of the *Cycloleberis* population.

CHAPTER 5

POPULATION BIOLOGY OF *HIPPOMEDON WHERO*

POPULATION DYNAMICS

DENSITY

The annual pattern of population density for *Hippomedon* (Fig. 5.1) shows an overall increase in abundance during spring to maximum densities between Dec. and Mar., and thereafter a decline to lowest densities during midwinter months. Densities increased by a factor of three from the July - Aug. minimum of 140 0.1 m^{-2} to about 450 0.1 m^{-2} over summer. Within this general pattern there are lesser fluctuations which, because of their regular recurrence, may be significant. In both years the spring-summer increase was interrupted during Nov. The summer plateau was broken by a fall in density during late Jan. - early Feb. and again low densities in Mar. - Apr. interrupted the otherwise steady decline to winter densities. It is possible that these fluctuations represent four distinct periods of recruitment in Oct., in Dec. - early Jan., in late Feb. - early Mar., and in late Apr.

POPULATION STRUCTURE

Careful analysis of the monthly population structure based on size-frequency data, and interpreted with the assistance of cumulative percentage curves plotted on probability paper following Harding (1949) and Cassie (1954), revealed that five cohorts were produced annually (Fig. 5.2). At any one time the population consisted of four cohorts and an additional cohort was present between March and May. Both males and females had similar patterns of growth and mortality and the overall pattern of cohort appearance, growth and disappearance was remarkably similar between years.

RECRUITMENT

Brooding females were present throughout the year but recruitment was significant only during the six months between Sept. and Mar. (Fig. 5.2). Recruitment to a cohort was not always discrete but spanned at least one month in many cases. Further, it appears that recruits to any one cohort may be derived from adults in more than one cohort. Thus there may be some degree of breeding synchrony between cohorts.

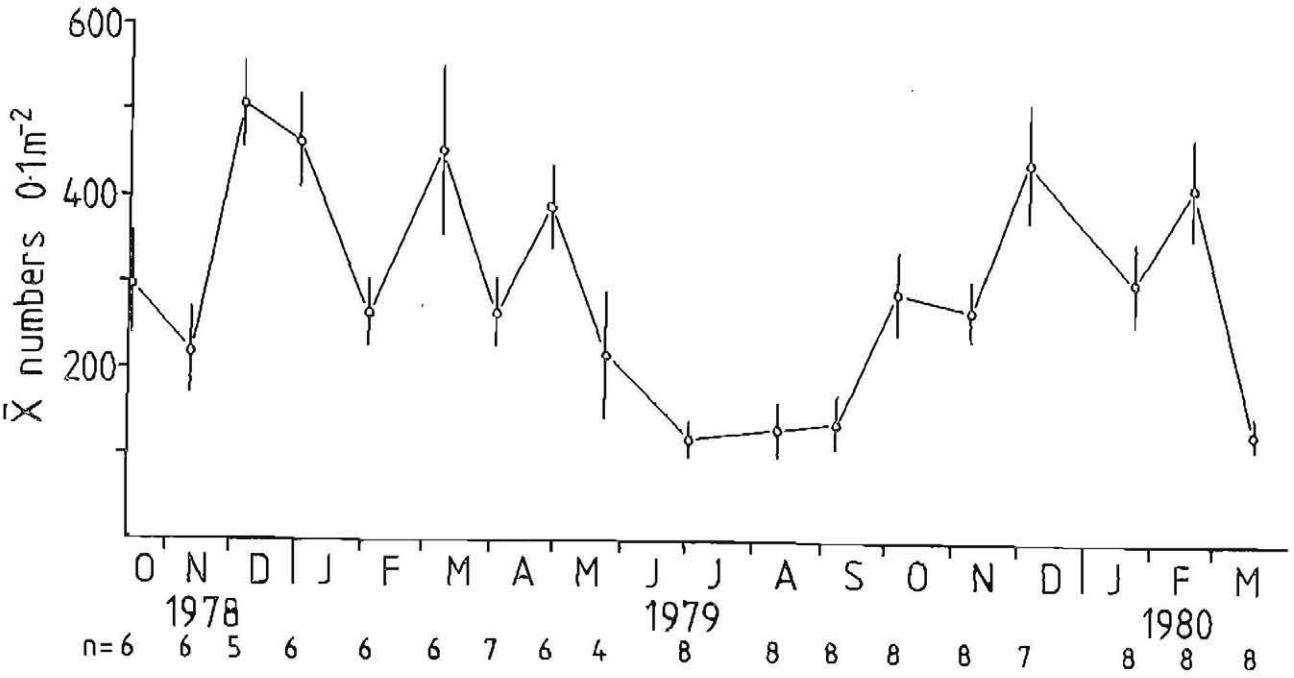

Fig. 5.1 Seasonal changes in mean (± 1SE) density of *Hippomedon*.

Large females predominantly of cohort A apparently produced recruits to cohort C in Oct. (probably beginning during Sept.) (Fig. 5.3). At the time of first sampling most broods of cohort B females were at an early stage of development. Some of these broods were released before, and most soon after the Nov. sampling date producing cohort D. A small number of cohort B females carried early embryos in Nov. that produced cohort E in Jan. At about this time a small number of cohort B females produced another brood that was carried through Feb. as mid to late embryos, and released by Mar. to produce cohort F following the disappearance of cohort A. Cohort C females maturing by Feb. probably contributed a small proportion of cohort F. Most cohort C females however, brooded embryos from early Mar. to initiate cohort G in late Apr. Following the loss of cohort B early in this month, reproductive activity all but ceased. Cohort D matured during Apr., carried broods during May, and disappeared from the population by July after contributing a very few offspring to cohort H. Similarly cohort C was not present after May. Growth of cohort H remained almost stationary until Oct. by which time its numbers had increased significantly through recruitment from cohorts E and F during Aug. and Sept. Cohort E was lost in Sept. Additional recruits from cohort F produced cohort I early in Nov. along with fewer recruits from cohort G. By late Jan. further recruits from cohorts F and G had established cohort

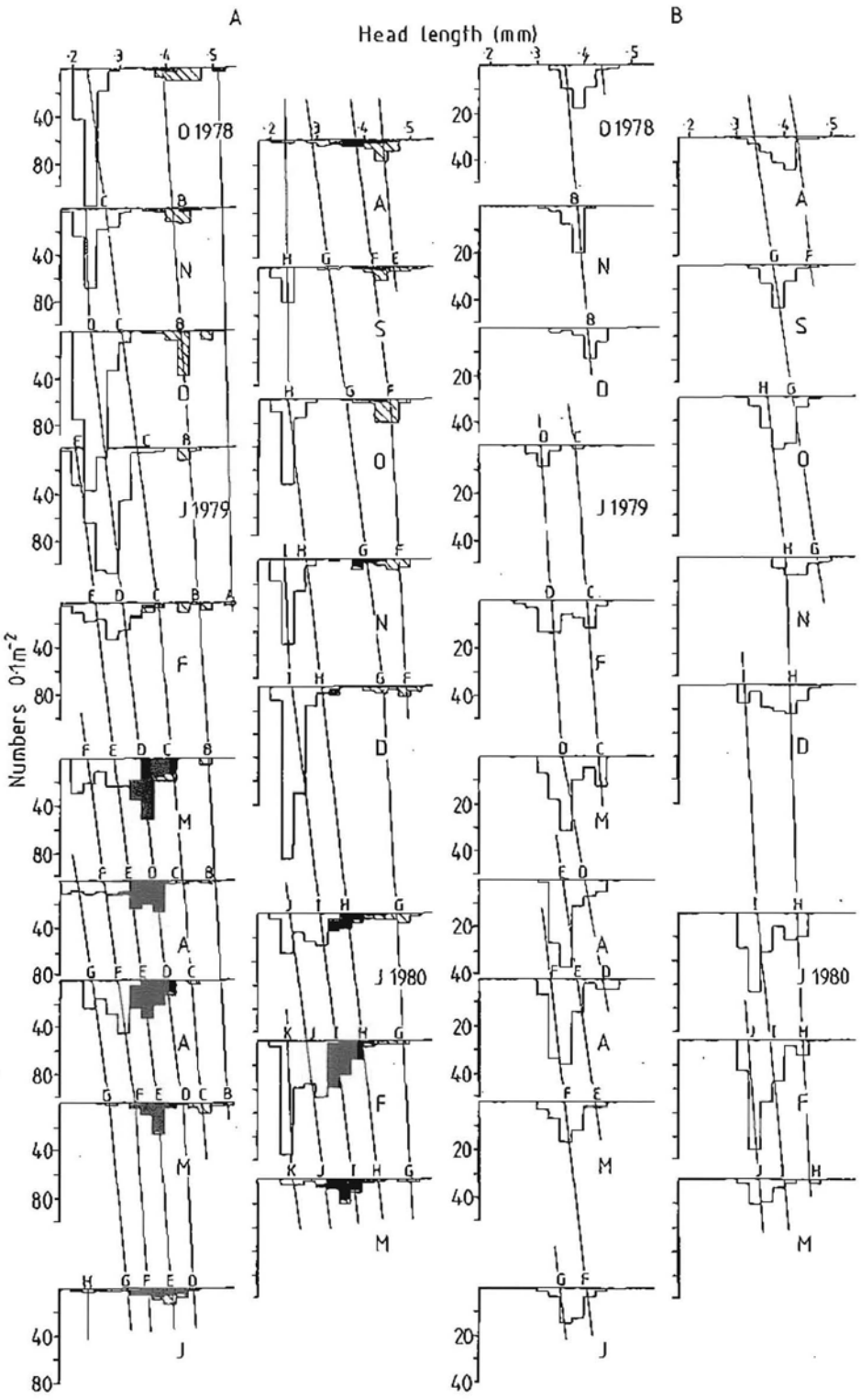

Fig. 5.2 Monthly changes in the *Hippomedon* population size-frequency composition for juveniles (unshaded), non-gravid (black) and gravid (hatched) females (A) and for males (B).

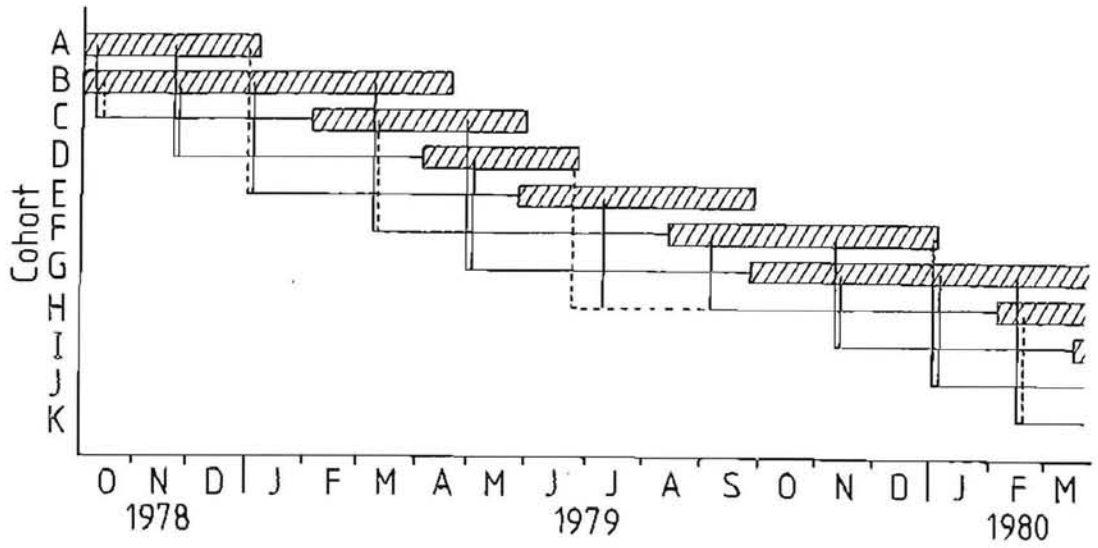

Fig. 5.3 Derivation, seasonal occurrence and egg production of each cohort of *Hippomedon* (shaded bars, gravid females; broken lines, minor contributions).

J as cohort F disappeared from the population. The appearance of cohort K, produced by cohorts G and H in Feb., marked the slowing of breeding activity for the summer. One month later there were few gravid females and no new recruits had been added. To complete the cycle of five cohorts produced per year observed in 1978-79, the females of cohorts G, H, and I carrying broods of mid-late embryos in Mar. presumably produced a further cohort in late Mar. - early Apr.

LONGEVITY AND MATURITY

Both Figs. 5.2 and 5.3 permit estimates of ages at maturity and maximum longevities. Maximum longevities varied seasonally and it seems that females may live longer than males in some cohorts (Table 5.1). Males of summer cohorts (C and D) lived for up to about 214 days, whereas those of over-wintering cohorts (E, F & G) lived for 256 - 363 days. Estimates for summer cohort females range between 214 and 244 days, and 260 - 363 days for over-wintering females of cohorts E, F and G.

Size and age at first breeding could not be determined for either sex and it must be assumed that males were sexually mature at 0.300 mm head

Table 5.1 Seasonal occurrence, estimated age at maturity and estimated maximum longevity of cohorts C - H of *Hippomedon* (overwintering cohorts bracketed).

Cohort		Seasonal occurrence	Estimated age at maturity (days)	Estimated maximum longevity (days)
C	♂	Oct. - Apr.	81	211
	♀	Oct. - May	91	244
D	♂	Nov. - May	84	214
	♀	Nov. - May	84	214
E	♂	Jan. - Sept.	113	260
	♀	Jan. - Sept.	113	260
F	♂	Mar. - Nov.	112	256
	♀	Mar. - Dec.	122	293
G	♂	4 Apr. - Mar.	182	363
	♀	4 Apr. - Mar.	182	363
H	♂	Sept. - Mar.+	137	?
	♀	Sept. - Mar.+	137	?

length (h.l.) when penes and calceoli appeared. Some females of this size possessed small oostegites but the size at maturity must be taken as 0.350 mm h.l., the size of the smallest females found brooding embryos. Not all females matured and reproduced at this size however; only 4.6% of the total 0.350 mm h.l. females were gravid but 97.6% of 0.450 mm h.l. females carried embryos (Table 5.2). Ages at maturity appear to be similar for both sexes (Table 5.1):

Table 5.2 Percent frequency of different size female *Hippomedon* brooding embryos.

	Female head length (mm)							
	0.350	0.375	0.400	0.425	0.450	0.475	0.500	0.525
% brooding	4.6	15.6	61.5	85.1	97.6	90.8	80.0	66.7
n	139	120	84	128	65	49	10	4

80 - 90 days for summer cohorts (C & D) and 113 - 182 days for over-wintering cohorts (E, F, & G). No evidence was found suggesting seasonal changes in size and age at maturity.

REPRODUCTION

OCCURRENCE OF BREEDING

Data in Figs. 5.2 and 5.3 also indicate that females surviving to 0.500 mm h.l. reproduce at least twice and possibly three or more times. Consideration of these data (Figs. 5.2, 5.3) reveals that each new cohort was derived from two or three cohorts of parents and that between summers equivalent cohorts were derived from equivalent parental cohorts. This suggests some degree of breeding synchrony between cohorts. Moore (1981) described rhythmic semi-lunar brood production during summer months for both *Corophium bonnellii* and *Lembos websteri*, but brood production in *Hippomedon* showed no relationship to lunar periodicity. There is however, an unusual relationship between brood production and the occurrence of storms during summer months (Oct. - early Apr.) (Fig. 5.4). Three peaks in the proportion of gravid females brooding early embryos are evident at increasing intervals following storms. Conceivably, storms stimulate brood production directly in those females in a state of physiological readiness, thus producing the first peak within two days. The second peak, some 9 - 11 days after the storms, possibly result when mature females capitalize on the greater abundance of fine detrital material generated by the storms to produce their broods. Similarly the lag of about 26 - 28 days

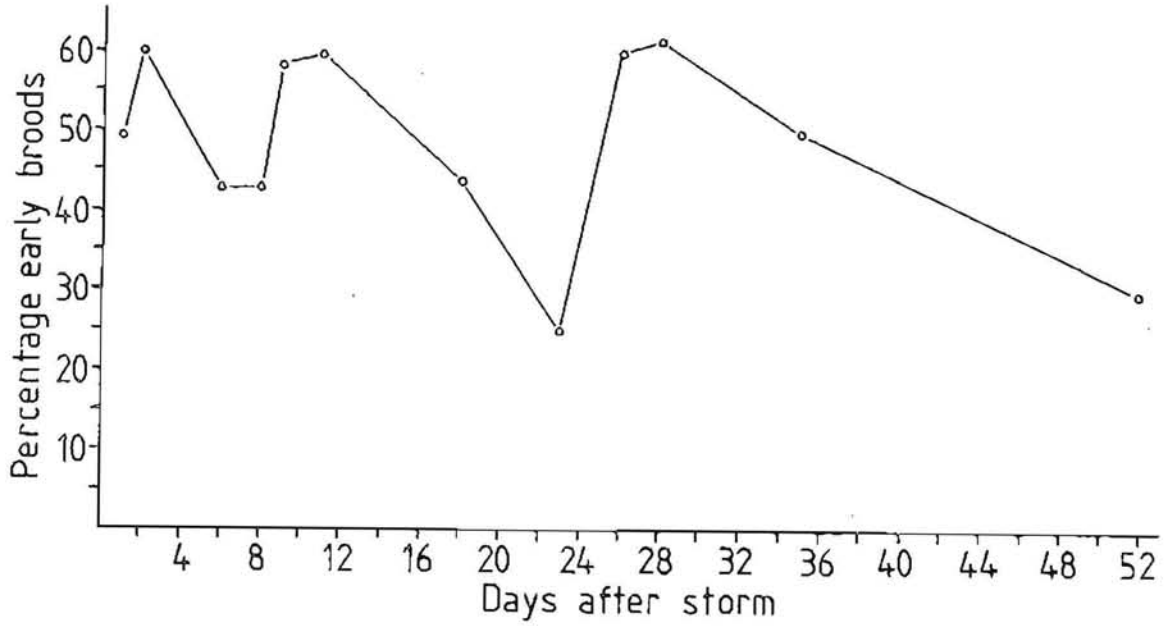

Fig. 5.4 Changes in the percentage of gravid females carrying early (stage 1 - 2) embryos after storms (waves >1.25 m high).

until the third peak of early broods could be due to a third group of females which, with the increased food availability, moulted before producing a brood.

From autumn the proportion of reproductive females (>0.350 mm h.l.) brooding increased to over 80% by Oct. and exceeded 90% in Dec., thereafter declining to about 20% by Feb. - Mar. (Fig. 5.5). Recruitment patterns, as seen from the density of early juveniles (h.l. .175 - .225 mm) in the population (Fig. 5.5), are similar with most recruitment occurring during the five months between Aug. and Jan. - Feb.

Analysis of the seasonal brood composition (Fig. 5.5) further emphasizes the long duration of egg production and recruitment annually. With few exceptions, broods containing embryos at each development stage were present throughout the year but distinct peaks of occurrence are obvious in spring and summer.

EMBRYONIC DEVELOPMENT

Several attempts to determine embryonic development rates in the lab. failed due to poor adult survival and because developing embryos in the brood

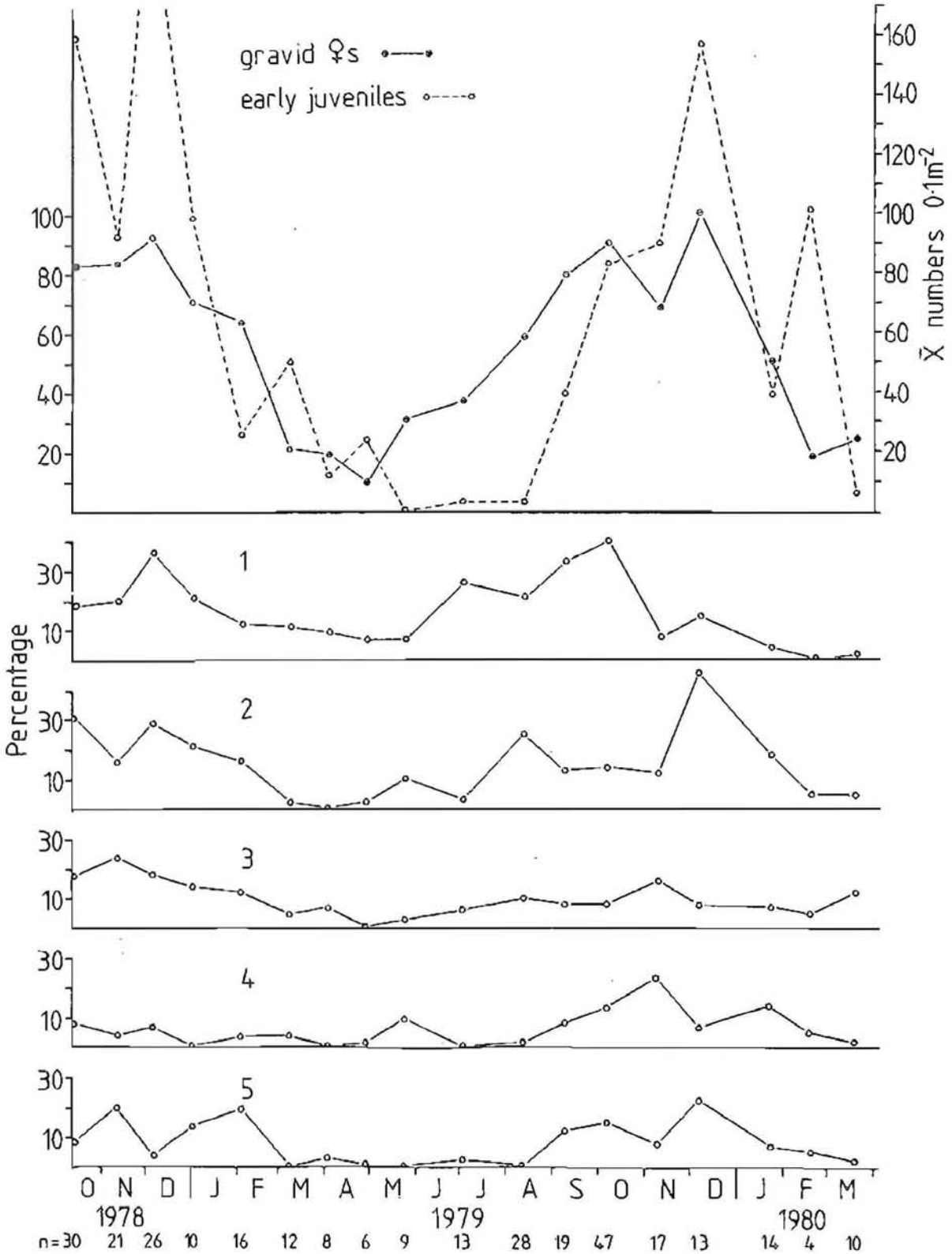

Fig 5.5 Seasonal changes in the percentage of reproductive females with broods (solid line), density of new recruits (broken line) and the percentage of broods at each development stage.

pouch were extremely difficult to see through the parents' coxae even when strongly illuminated from beneath (see Appendix 2.1). Consequently, embryonic development rates must be extrapolated from data in Fig. 5.5. Development times estimated by following the peaks of occurrence of successive development stages and of early juveniles ranged between 58 days ($\bar{x}$ temp. = 16.1°C) and 96 days ($\bar{x}$ temp. 10.7°C) (Table 5.3). Van Dolah *et al.* (1975) established a relationship between development time and temperature for marine and freshwater species of *Gammarus* and *Hyallela*. When compared with their curve plotted on log-linear paper, all estimates for *Hippomedon* lie above the line (Fig. 5.6). The estimates for stage 1 to stage 5 however, approximate a straight line parallel to the line for *Gammarus* and *Hyallela*, but some distance above it. Assuming this line

Table 5.3 Estimated and corrected embryonic development times for *Hippomedon* from data in Fig. 5.5.

Stage 1	Stage 5	Early juveniles	Duration (days)	$\bar{x}$ Temp (°C)
Dec. '78	Feb. '79		58	16.14
July '79	Oct. '79		96	10.73
Oct. '79	Dec. '79		61	14.16
Dec. '78		Mar. '79	92	16.4
July '79		Sept. '79	66	10.35
Oct. '79		Dec. '79	62	14.4
Dec. '79		Feb. '80	75	16.6

approximates a true relationship between embryonic development time and temperature for *Hippomedon*, then for a given temperature *Hippomedon* embryos take about 3.4 times longer to develop than embryos of *Gammarus* spp. and

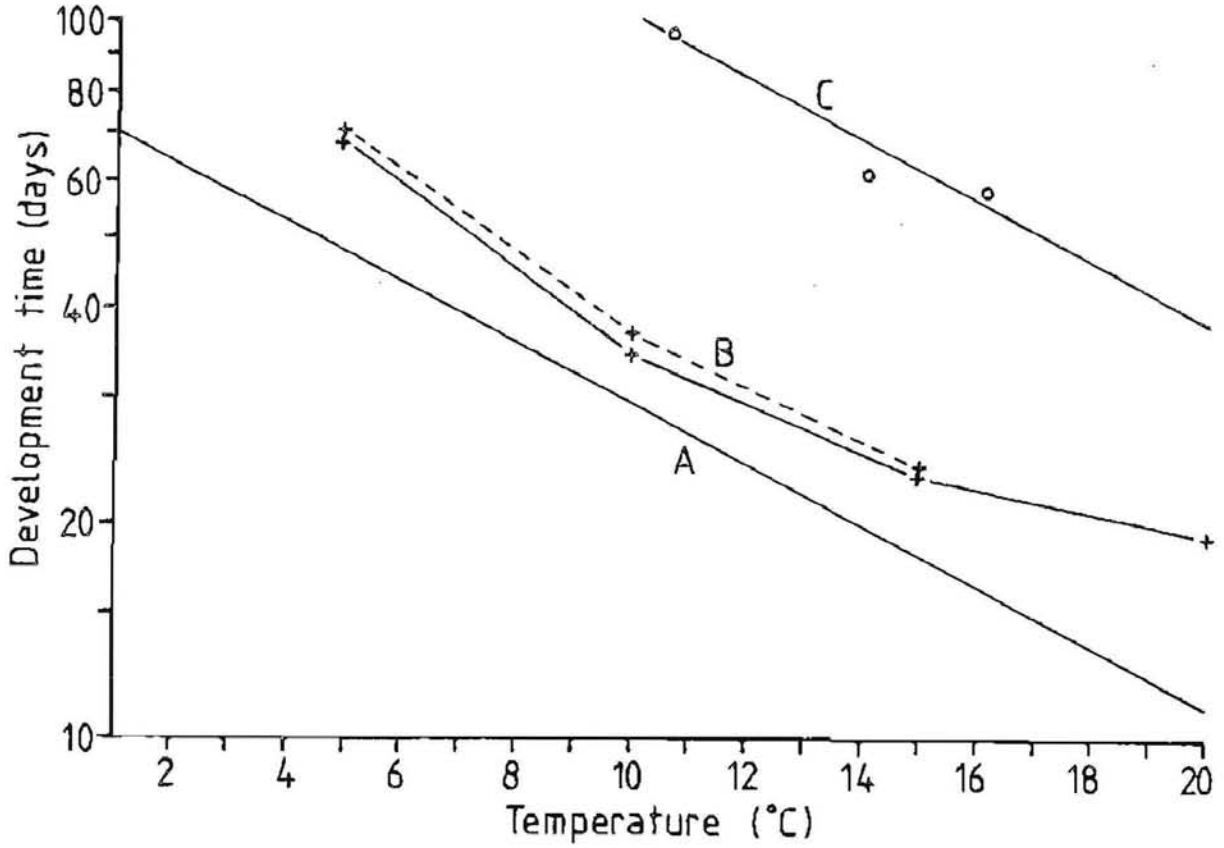

Fig. 5.6 Relationships between temperature and duration of embryonic development for amphipods: A, *Gammarus* and *Hyallela*; B, *Gammarus pulex*, lab. and field (broken line) data; C, estimate for *Hippomedon*.

Hyallela azteca. Welton & Clarke (1980) described a complex relationship between temperature and the duration of ontogeny in the freshwater *Gammarus pulex* and their estimates from field and laboratory data are included in Fig. 5.6. This also indicates that estimates of embryonic development time for *Hippomedon* are seriously in error.

During development the mean embryo length increases significantly by 70.92% from 0.434 mm in stage 1 to 0.612 mm in stage 4 (Table 5.4). Similarly, the observed 50.21% increase in volume (using the ellipsoid formula) between stages 1 and 4 was significant (Table 5.4). Seasonal mean egg (stage 1) lengths were determined from combined data for months grouped in threes on the basis of seawater temperatures (Fig. 2.2). Within each group there were no significant differences between monthly mean egg sizes (Appendix 2.2) and,

Table 5.4 Changes in mean length and volume of embryos during development for *Hippomedon*.

	Development stage				
	1	2	3	4	5 (head length)
$\bar{x}$ length (mm)	.434	.469	.506	.612	.206
SD	.034	.047	.068	.067	.020
n	226	189	131	100	68
	t = 8.538	t = 5.398	t = 11.837		
	p <<.001	p <<.001	p <<.001		
			t = 25.172		
			p <<.001		
$\bar{x}$ volume (mm^3)	.0233	.0285	.0267	.0468	
SD	.0032	.0112	.0063	.0133	
n	53	45	22	26	
	t = 3.012	t = .840			
	p .01-.001	n.s.			
			t = 5.909		
			p <<.001		
			t = 8.884		
			p <<.001		

although some seasonal differences are apparent (Appendix 2.3), there was no obvious seasonal pattern of egg size variation. Regression analysis revealed a negative relationship between egg size and sea temperature ($y = 0.5964 + -0.1029X$, $r = -0.4630$) which was not quite significant ($r_{(0.05)} = -0.482$) indicating that egg size is related to a combination of temperature and some other factor. The mean egg size for the 1978-79 summer was significantly smaller than for all other times, including the 1979-80 summer. Eggs of the 1978 spring did not differ significantly in mean size compared with eggs produced in the following spring, but they were significantly larger than eggs of the 1978-79 summer and smaller than winter eggs.

BROOD SIZE

Female *Hippomedon* brood between one and eight eggs and the overall mean brood size was 3.356 eggs (SD = 1.529, n = 320). As with other amphipods, there is a positive relationship between adult female size and the number of eggs (development stage 1 - 2) brooded described by the regression equation $Y = -5.968 + 21.43X$ ($r = 0.955$, $p < .001$). Seasonally the mean brood size (stage 1 - 2 embryos only) fluctuated between about 1.5 and 5 embryos and it exceeded three embryos per female during Sept. to Jan. (Fig. 5.7). The seasonal change in mean size of brooding females followed a very similar pattern (Fig. 5.7), but the degree of correlation between seasonal mean brood size and seasonal mean brooding female size was not quite significant at the .05 level ($r = 0.405$, dfs = 16). This suggests that the month to month changes observed for mean brood size result, in part, from changes in the size of brooding females and hence their ability to produce and/or carry eggs.

BROOD MORTALITY

Combined data on changes in brood size with stage of development reveal 14.2% brood mortality between stages 2 and 4 (Table 5.5), but this was not statistically significant. Brood mortality should be calculated from changes in numbers of embryos between broods at the second and penultimate stages of development to minimize errors resulting from incomplete stage 1 and stage 5 broods. In *Hippomedon* for example, the mean number of embryos in stage 1 broods was lower than the mean number in stage 2 broods, but not significantly so (Table 5.5). There was a significant difference

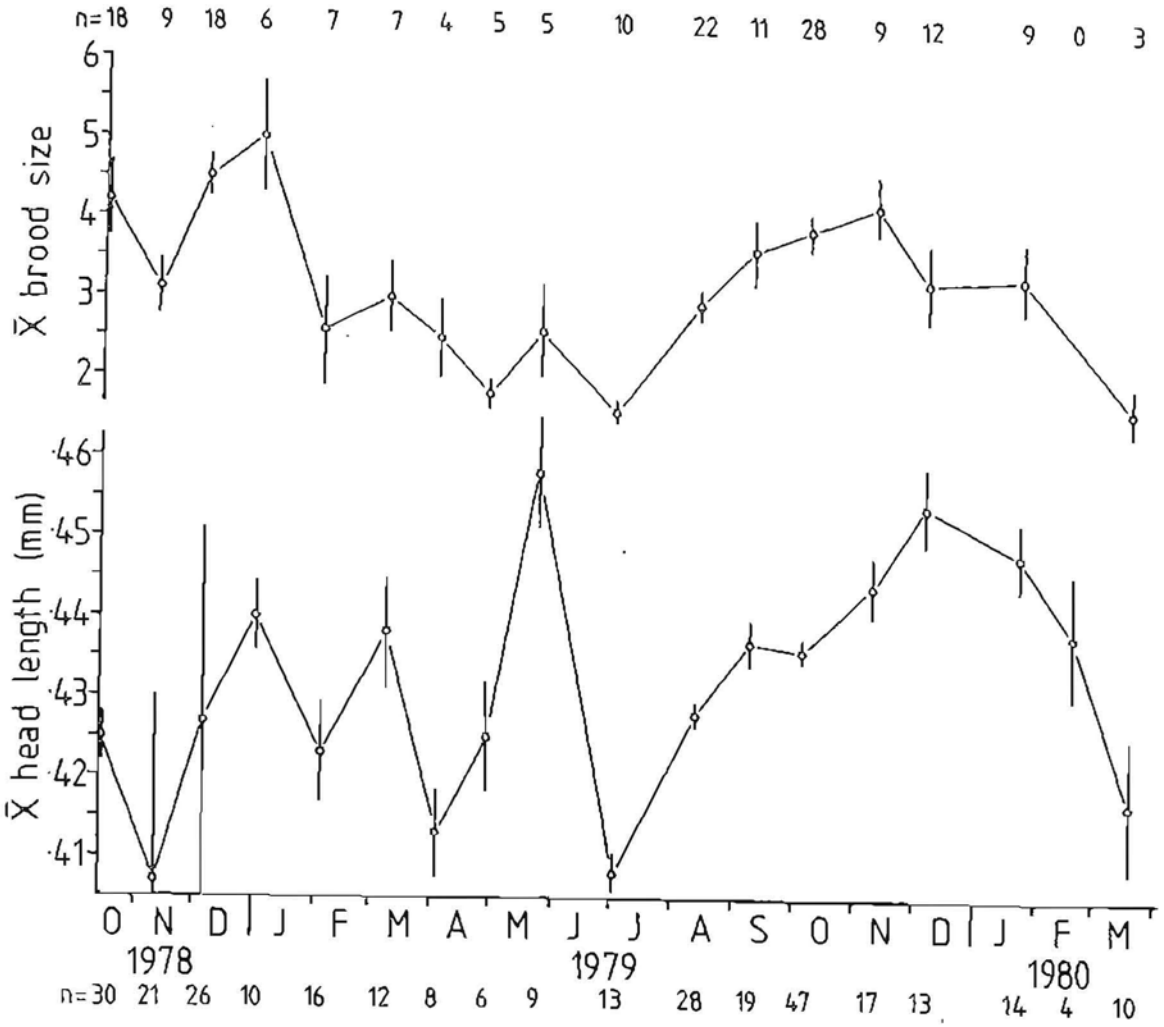

Fig. 5.7 Seasonal changes in the mean (± 1SE) brood size (stage 1 - 2 broods only) and in the mean (± 1SE) size of gravid females.

between the mean size of stage 4 and stage 5 broods however, and this would increase the estimated brood mortality to 27.05%. Thus it is preferable to use the change in mean brood size between stages 2 and 4 to provide a conservative estimate of brood mortality. Brood mortality in *Hippomedon* females is assumed to be independent of size and season since there are too few data for a realistic analysis of this question (Appendicies 2.4, 2.5).

SEX RATIO

Quite remarkable fluctuations occur in the month to month sex ratio (♂:♀) of the South Bay *Hippomedon* population (Fig. 5.8). In only one month

Table 5.5 Brood size at each stage of embryonic development in *Hippomedon*.

	Development Stage				
	1	2	3	4	5
$\bar{x}$	3.283	3.630	3.345	3.116	2.395
SD	1.526	1.520	1.470	1.366	1.386
n	99	81	58	43	38
			t = 1.917 n.s.		
		t = 1.521 n.s.		t = 2.352 n.s.	

(Jan. 1979) were there more females than males and on three occasions males outnumbered females by more than three to one. These disparities were only partly due to my ability to identify males at a smaller size than females and juveniles could be distinguished; the broken line in Fig. 5.8 shows monthly sex ratios calculated after excluding data for size classes containing juveniles. Generally, the peaks of male predominance coincided with peaks in the percent of gravid females carrying newly hatched young (stage 5 embryos) and, to a lesser extent, with the percentage of early juveniles in the population (Fig. 5.8). In iteroparous amphipods where broods are produced in close succession, amplexus, female moulting and copulation occur soon after release of the previous brood (Mills, 1967; Myers, 1971). Thus the increases in male predominance (sex ratio) occurred at about the time of hatchling release when many females would be ready to moult and to produce new broods of eggs requiring fertilization. Immigration of males into the study area does not seem to be the cause of these fluctuations because changes in sex ratio were not accompanied by changes

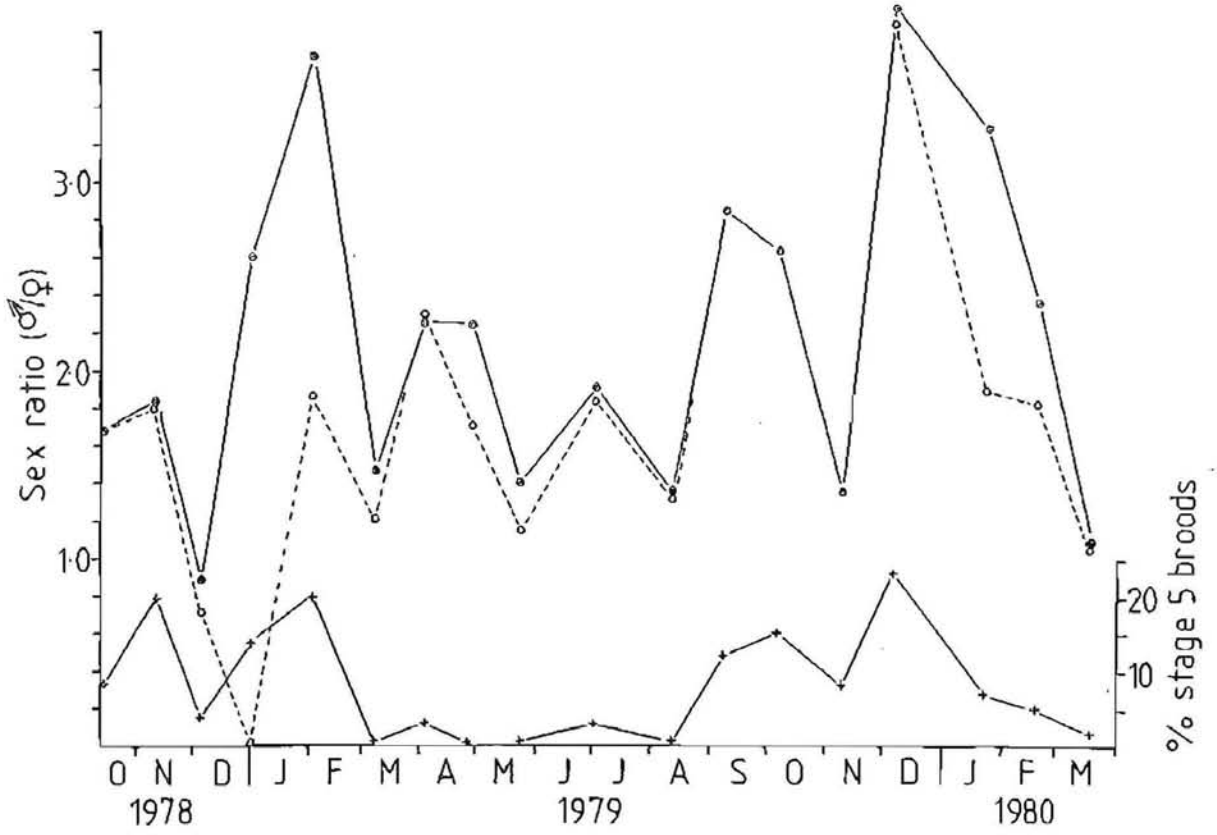

Fig. 5.8 Seasonal changes in sex ratio of the total population and the total population excluding size classes containing juveniles (broken line), and seasonal changes in the percentage of broods at development stage 5.

in population density. Thus male *Hippomedon* exhibit a moulting and breeding periodicity synchronized with that of females and probably mediated by the same stimuli.

Sex ratio data are often examined by plotting the percentage of males in successive size classes to derive a probability curve following Wenner (1972). This approach however, either has not been applied to species populations which include an unsexable juvenile fraction or considers only the sexable portions of populations. When unsexable juveniles are included, the curve for *Hippomedon* males (Fig. 5.9A) is bell-shaped reaching a peak of 76% males at 0.325 mm h.l. The percentage of males declines steeply to zero at 0.450 mm h.l. with only females in the three largest size classes.

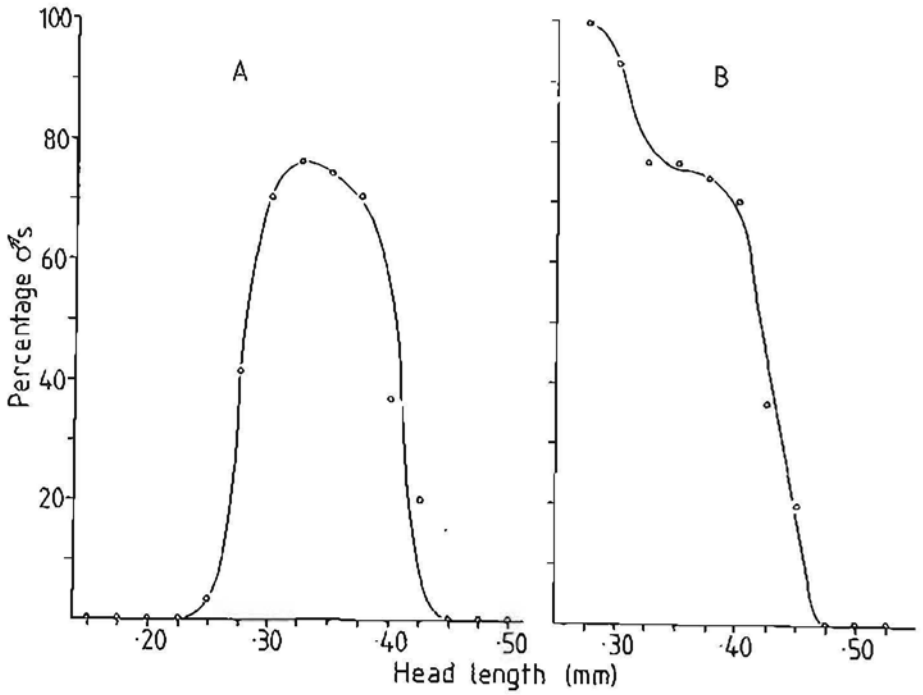

Fig. 5.9 Percent frequency of males in each size class including unsexable juveniles (A) and for sexable individuals only (B).

The right-hand portion of the curve fits Wenner's "intermediate pattern" and accordingly implies protandric sex reversal, but this sex reversal would be only partial because males never constitute more than 76% of the population. About 24% of individuals thus would mature directly into females whereas the bulk of individuals would mature as males and later develop into females. When sexable individuals only are considered, the resultant probability curve (Fig. 5.9B) approximates that for *Pandalus hypsinotus*, also considered to be of the "intermediate pattern" and indicative of partial hermaphroditism (Wenner, 1972).

Partial sex reversal does not seem very likely in *Hippomedon* however, and I consider that the use of percent size-frequency distributions of males (or females) for examining sex ratios may be very misleading because the shape of the curve is greatly dependent upon the growth rate between size classes and both sexes maturing at a similar size. Recently Haley (1979) reinvestigated *Hippa pacifica*, a species described by Wenner (1972) as exhibiting the "intermediate" probability curve. Haley's work produced a similar probability curve, but histological work produced no evidence of

sex reversal. Instead, his experimental growth studies showed that the maximum size attained by males was smaller, and that with increasing size they moulted less frequently and had smaller moult increments than females. These factors adequately explained the observed sex-size pattern of *Hippa pacifica* and similar factors may be operating for *Hippomedon*.

Where data on moult increments and moult frequency are lacking, a more informative approach is to examine the size-frequency distributions of juveniles, males, females (Fig. 5.10). Since these data were collected by quantitative, random sampling, a decrease in the total number of individuals in successive size classes must be expected as a consequence of mortality. Instead we find elevated numbers of individuals within the 0.300 - 0.375 mm h.l. range that can be explained only by a decreased growth rate of individuals approaching this size. Further, because most individuals within this size range are males, it seems that their growth rate must decrease with increasing size and that the age distribution of males in any of these size classes must be greater than for females of the same size.

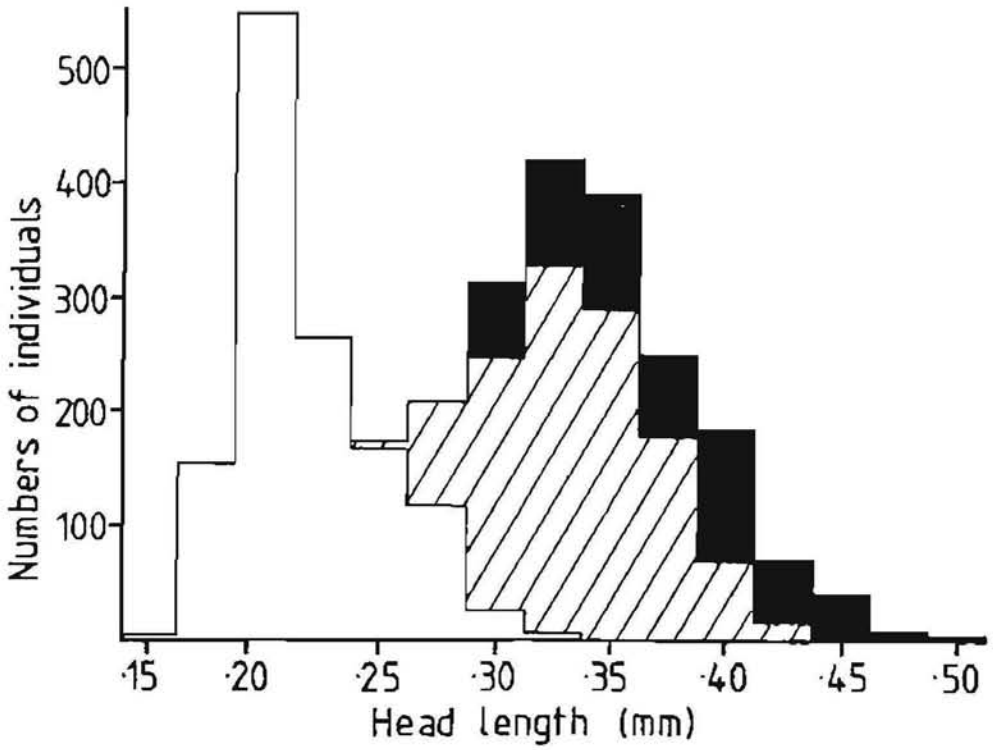

Fig. 5.10 Population size frequency composition Oct. 1978 - Mar. 1980; unshaded, juveniles; hatched, males; black, females.

These factors alone however, do not fully explain the observed overall sex ratio of 2.09 in favour of males. Since it is not possible to sex young individuals when they first enter the population, it must be assumed that either the sex ratio at recruitment is 1:1 and there is selective mortality of or emigration by females, or the sex ratio of hatchlings is biased in favour of males. The disparity seems too great to be attributed simply to emigration and selective mortality.

CHAPTER 6

POPULATION BIOLOGY OF *PATUKI ROPERI*

POPULATION DYNAMICS

DENSITY

Seasonally the mean population density of *Patuki* (Fig. 6.1) follows the expected pattern of highest densities during summer and lowest during winter. Densities ranged between 40 0.1 m^{-2} in May 1979 and 580 0.1 m^{-2} in Dec. 1978. Generally three annual peaks were apparent and these seemed consistent between years; a small, early spring peak in Aug. - Sept., an early summer maximum in Nov. - Dec., and a variable autumn peak between late Feb. and Apr. In 1978 the summer peak was almost double that of the following summer, but it exceeded 280 0.1 m^{-2} for only two months compared with three months in 1979. Both years were characterised by a sharp decline from the summer peak to about 130 - 170 0.1 m^{-2} in Jan. Thereafter followed the autumn increase to 200 - 240 0.1 m^{-2}, the duration of which varied between years. As a result of this variation the winter minimum may occur between Mar. and May, and the timing of the spring increase may also vary with these two events.

POPULATION STRUCTURE

Analysis of the monthly population structures (Fig. 6.2A,B) showed that at any one time the population consisted of 7 - 10 cohorts of which two or more carried embryos, and that 11 - 12 cohorts were produced annually. Males (Fig. 6.2B) attained a smaller maximum size than females and grew more slowly. The steeper lines joining each male cohort at successive times and their closer spacing along the x-axis indicate that their slower growth rate results from smaller moult increments, a lower moulting frequency, or both.

Estimates of female age at puberty (first appearance of oostegites), and age at maturity and maximum longevity for both sexes from several cohorts based on Fig. 6.2 are in Tables 6.1 and 6.2. Females of over-wintering cohorts (J-O) reached puberty at 69 - 133 days compared with 44 - 82 days for summer cohorts (F-I, P-U). Similarly, the estimated ages at maturity and maximum longevities differed for females of summer and winter cohorts. Summer cohorts matured at 56 - 113 days and lived for up to 147 - 177 days

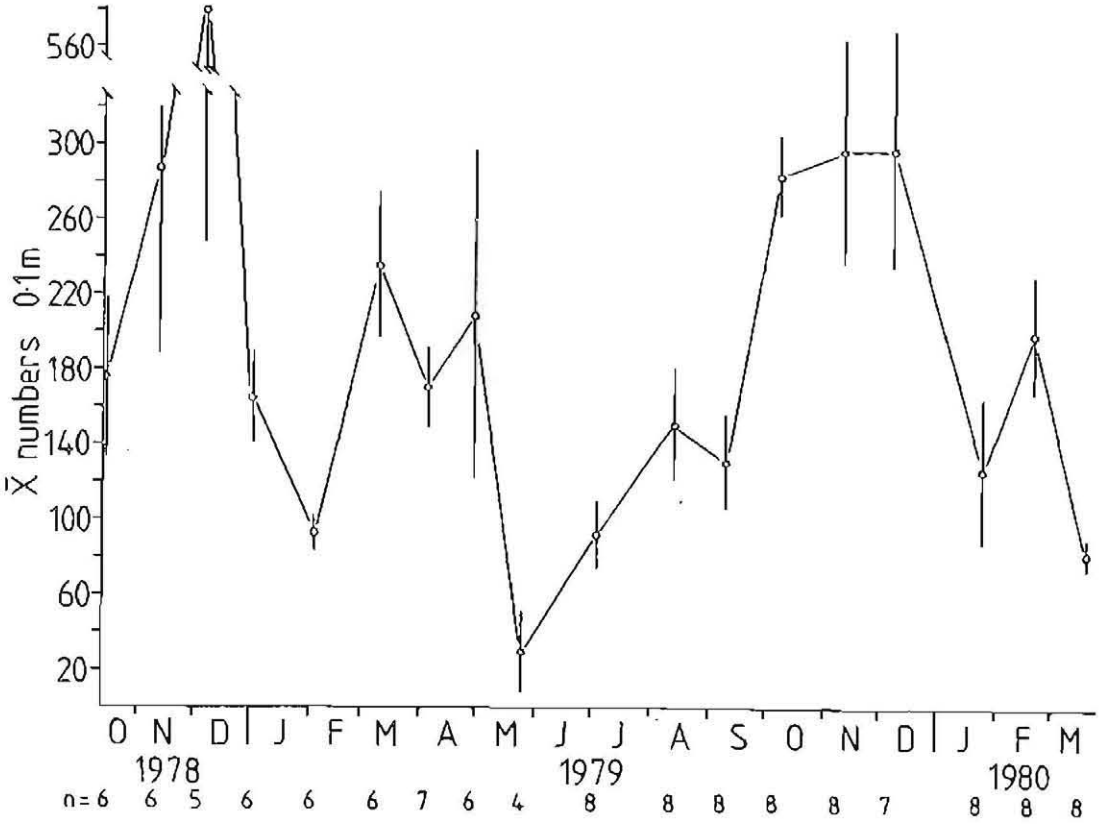

Fig. 6.1 Seasonal changes in mean (± 1SE) density of *Patuki*.

compared with 117 - 166 and 195 - 271 days respectively for winter cohorts.

Table 6.2 shows that although the size at maturity is taken as 0.800 mm h.l., the smallest females found carrying embryos, the majority of females do not produce broods until about 0.900 mm h.l. Over 60% of all females larger than 1.000 mm h.l. carried broods.

Because males apparently grow more slowly than females, juvenile males which could not be recognized as such may also have a slower growth rate. Consequently ages at maturity and maximum longevities for males (Table 6.3) are probably underestimated. Despite this, differences between summer and winter cohorts are apparent; males mature when younger than and do not live as long as females. The estimated age at maturity seems greater for winter cohorts (L-O) and their maximum longevities range between 147 - 186 days compared with 56 - 139 days for summer cohorts (F-K, P-U).

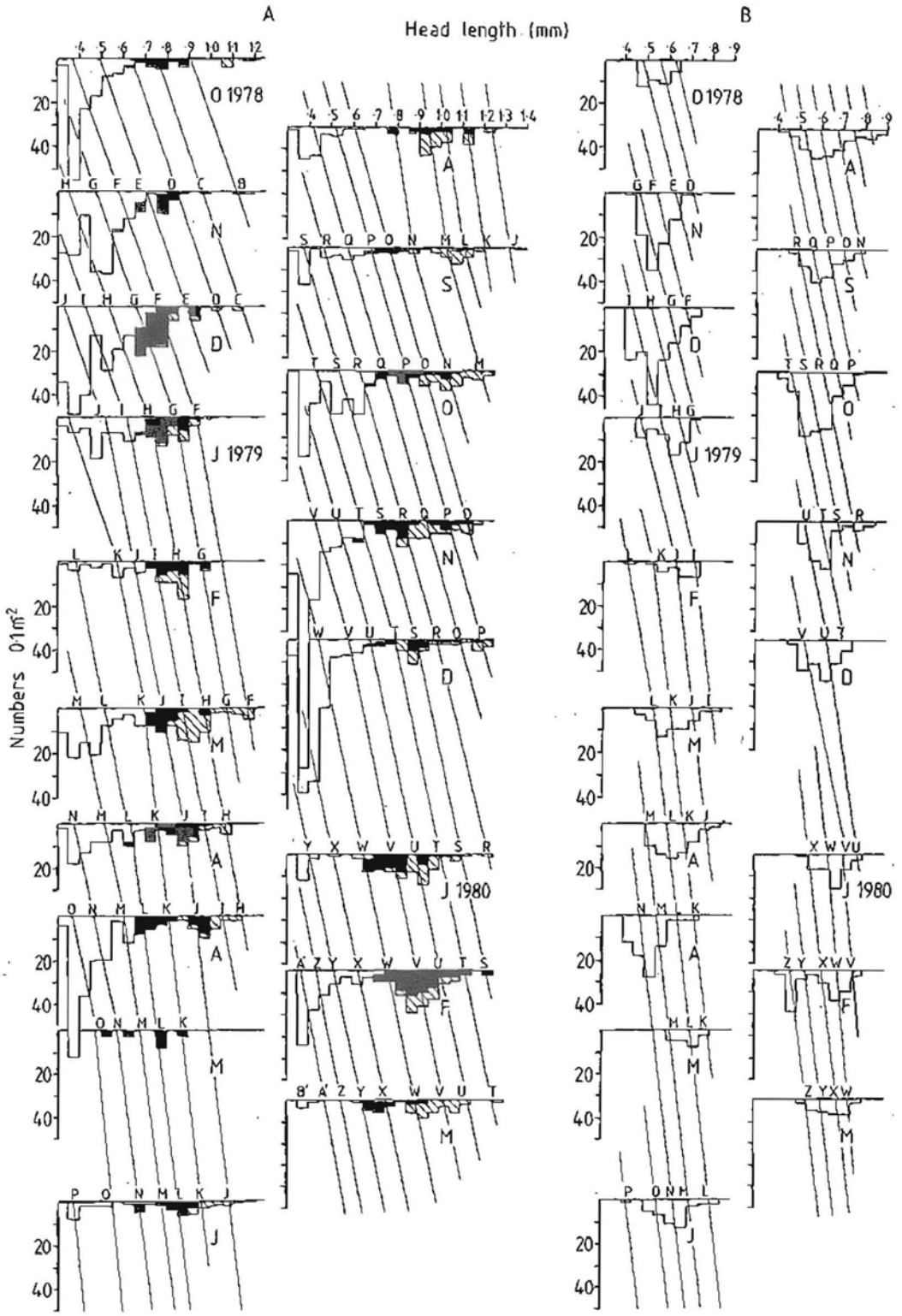

Fig. 6.2 Seasonal changes in the *Patuki* population size-frequency composition for juveniles (unshaded), non-gravid (black) and gravid (hatched) females (A) and for males (B).

Table 6.1 Seasonal occurrence, estimated age at puberty (appearance of oostegites), estimated age at maturity (first brood production) and estimated maximum longevity of female *Patuki* of cohorts F-U (from Fig. 6.2A) (overwintering cohorts bracketed).

Cohort	Seasonal occurrence	Estimated age at puberty (days)	Estimated age at maturity (days)	Estimated maximum longevity (days)
F	Oct.-Mar.	56	56	147
G	Oct./Nov.-Mar./Apr.	41	66	145
H	Nov.-late Apr.	51	67	168
I	Nov./Dec.-May	71	82	177
J	Dec.-Sept.	74	117	271
K	Jan.-Sept.	79	139	246
L	Feb.-Sept./Oct.	69	145	227
M	Mar.-Oct.	73	166	208
N	Apr.-Oct./Nov.	86	154	199
O	late Apr.-Nov.	133	161	195
P	July-Dec.	82	113	157
Q	Aug.-Dec./Jan.	55	72	164
R	Aug./Sept.-Jan.	58	75	150
S	Sept.-Feb.	62	75	164
T	Oct.-Mar.	48	61	165
U	Oct./Nov.-Mar+	44	68	>148

Table 6.2 Percent frequency of different size females brooding embryos.

Female size class (h.l., mm)	% brooding	n
.650	0	4
.700	0	36
.750	0	58
.800	7.2	83
.850	28.2	78
.900	54.3	105
.950	60.8	102
1.000	64.2	67
1.050	73.8	42
1.100	75.6	41
1.150	77.4	31
1.200	82.4	17
1.250	87.5	8
1.300	100.0	1
1.350	-	0
1.400	100.0	1

REPRODUCTION

BREEDING AND RECRUITMENT

Fig. 6.3 summarises much of the information in Fig. 6.2 and Tables 6.1, 6.2 and identifies the probable parental cohorts of each new cohort. This shows that recruits to a cohort may be contributed by two to four (five in one case) parent cohorts and that females of a cohort may supply recruits to up to four cohorts.

Breeding was almost continuous with gravid females present at all times. Recruitment to new cohorts occurred throughout the year, but there was wide variation in the numbers of juveniles actually entering the population in each cohort (Fig. 6.4). Nov. - Dec. was the time of peak recruitment and corresponds to the time of maximum population densities (Fig. 6.1) and the

Table 6.3 Seasonal occurrence, estimated age at maturity (appearance of penes), and estimated maximum longevity of male *Patuki* of cohorts F-U (from Fig. 6.2B) (overwintering cohorts bracketed).

Cohort	Seasonal occurrence	Estimated age at maturity (days)	Estimated maximum longevity (days)
F	Oct.-Dec.	15	56
G	Oct./Nov.-Jan.	15	76
H	Nov.-Jan./Feb.	13	80
I	Nov./Dec.-Mar.	13	104
J	Dec.-Apr.	25	117
K	Jan.-May	16	139
L	Feb.-Aug.	16	186
M	Mar.-Aug./Sept.	26	167
N	Apr.-Sept.	21	154
O	late Apr.-Sept./Oct.	20	147
P	July-Oct.	20	96
Q	Aug.-Oct./Nov.	14	72
R	Aug./Sept.-Nov.	13	75
S	Sept.-Nov./Dec.	14	76
T	Oct.-Dec./Jan.	17	85
U	Oct./Nov.-Jan.	17	92

period when cohorts were produced most frequently (Figs. 6.2, 6.3). A second minor peak of recruitment occurred in Feb. - Mar. and a larger one in Apr. - May when the total population density was declining (Fig. 6.1).

Some degree of breeding synchrony between cohorts is apparent (Fig. 6.3) because recruits entered each new cohort from the 2 - 4 parental cohorts apparently simultaneously at 20 to 54 day intervals. A lunar periodicity of

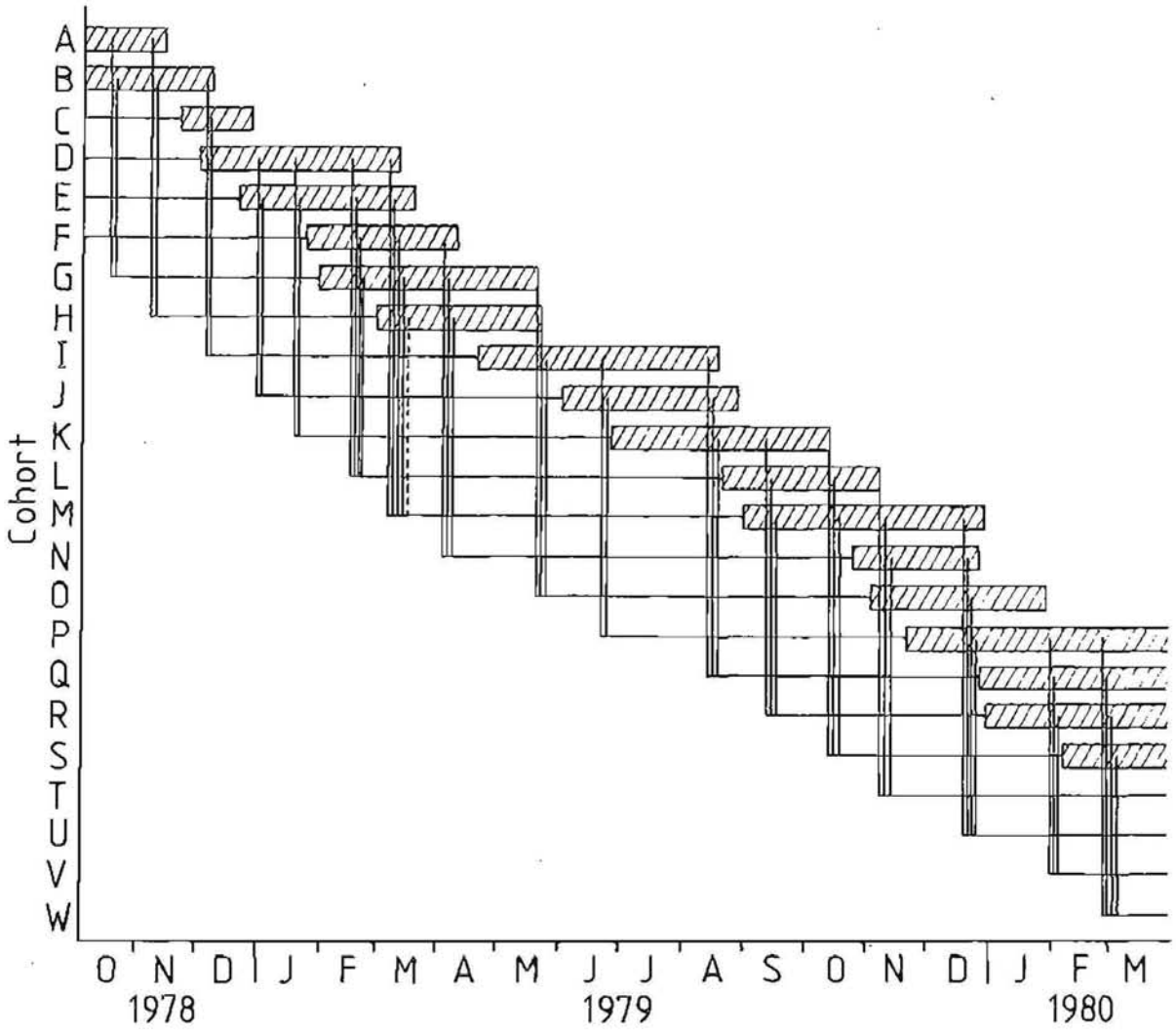

Fig. 6.3 Derivation, seasonal occurrence and egg production of each cohort of *Patuki* (shaded bars, gravid females; broken lines, minor contributions).

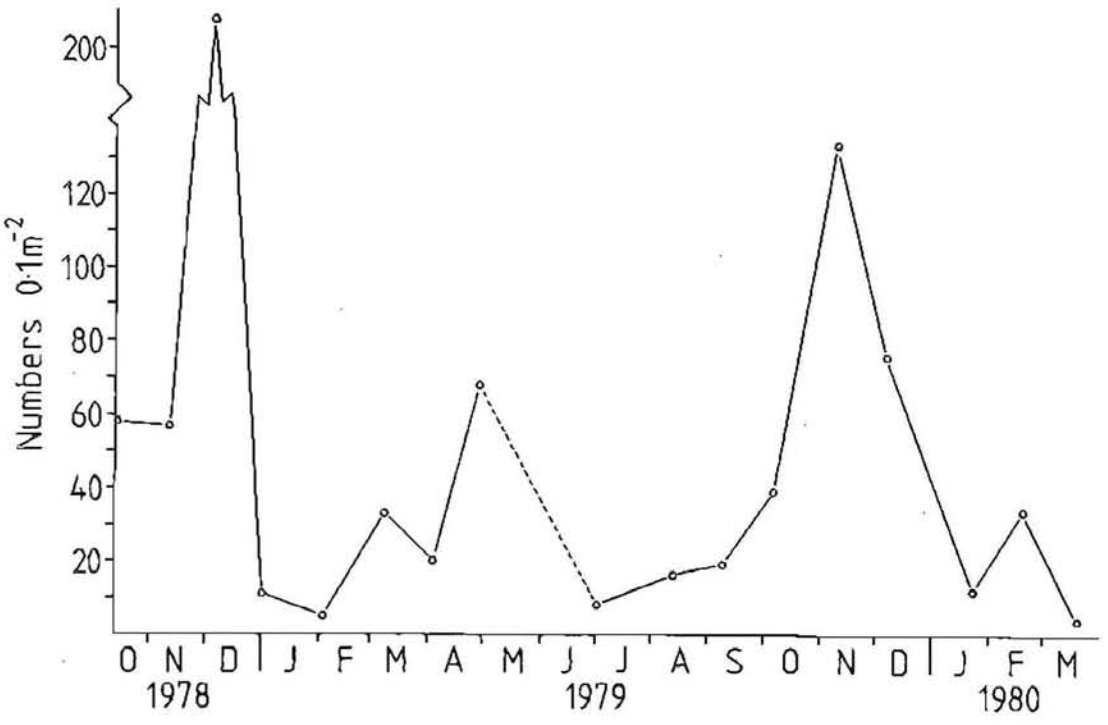

Fig. 6.4 Seasonal densities of early (<.400 mm h.l.) juvenile *Patuki*.

breeding activity is indicated by regression analysis of the percentage of gravid females carrying new broods (stage 1 - 2 embryos) at 14 - 27 days after the last full moon (Fig. 6.5A). This periodicity is however, strangely modified by the occurrence of storms (wave height >1.25 m). Immediately after storms about 75% of broods are new (Fig. 6.5B) and the percentage of new broods produced declines steadily thereafter. The lunar event synchronizing breeding activity may be the new moon, 14 - 15 days after full moon. At this time nights will be darkest and individuals may enter the night plankton for amplexus, mating and brood production with minimal risk of capture by nocturnal predators. Conceivably, the intensity of reproductive activity is determined by food availability such that after storms when algal and terrestrial plant detritus abound in the habitat, most non-gravid females will mate and produce a brood at the next new moon.

The percentage of reproductive females carrying broods each month (Fig. 6.6) exhibits a similar seasonality to that of early juveniles in the population (Fig. 6.4). A marked decline in females brooding preceeded the 1978 summer peak of recruitment. As the numbers of new recruits declined sharply, the proportion of brooding females increased correspondingly to a

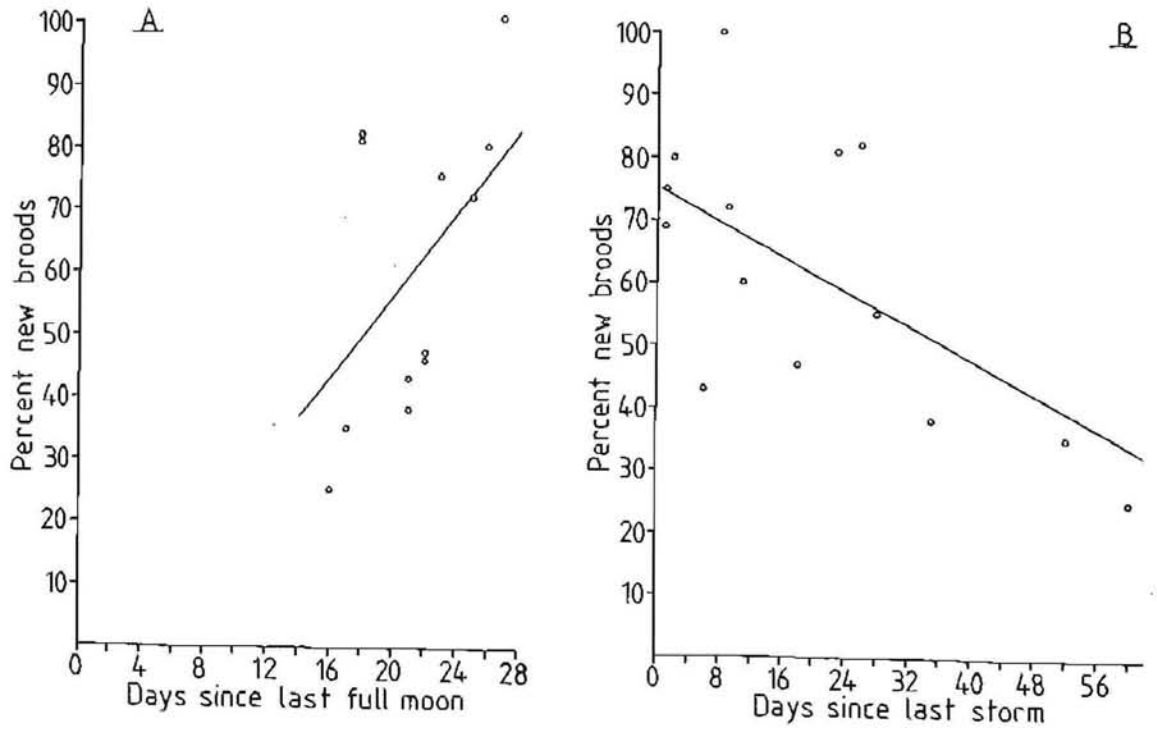

Fig. 6.5 The effect of time since last full moon (A) and time since last storm (waves >1.25 m high) (B) on the percentage frequency of new (stage 1 - 2) broods (A, $Y = -9.000 + 3.25X$, $r = 0.570$, $p = .05$; B, $Y = 75.390 - 0.691X$, $r = -0.669$, $p < .01$).

maximum before the autumn peak of recruitment. A similar situation ensued during the following summer but the percentage of females brooding did not decline with the end of the summer peak of recruitment. Indeed, the 1979-80 recruitment decline (Fig. 6.4) in Dec. - Jan. commenced before a period of severe storms (wave height >2.5 m) (Fig. 3.3) whereas more than 60% of mature females carried broods until after the storms had passed (Fig. 6.6). This decline was to about 35% brooding in mid-Feb., was brief, and by mid-Mar. over 80% of females carried broods (Fig. 6.6). These observations indicate that the stormy periods, beginning in mid-Dec. stimulated production of four successive broods, the last of which was carried until about early Mar.

Embryos at all stages of development occurred in most months and the

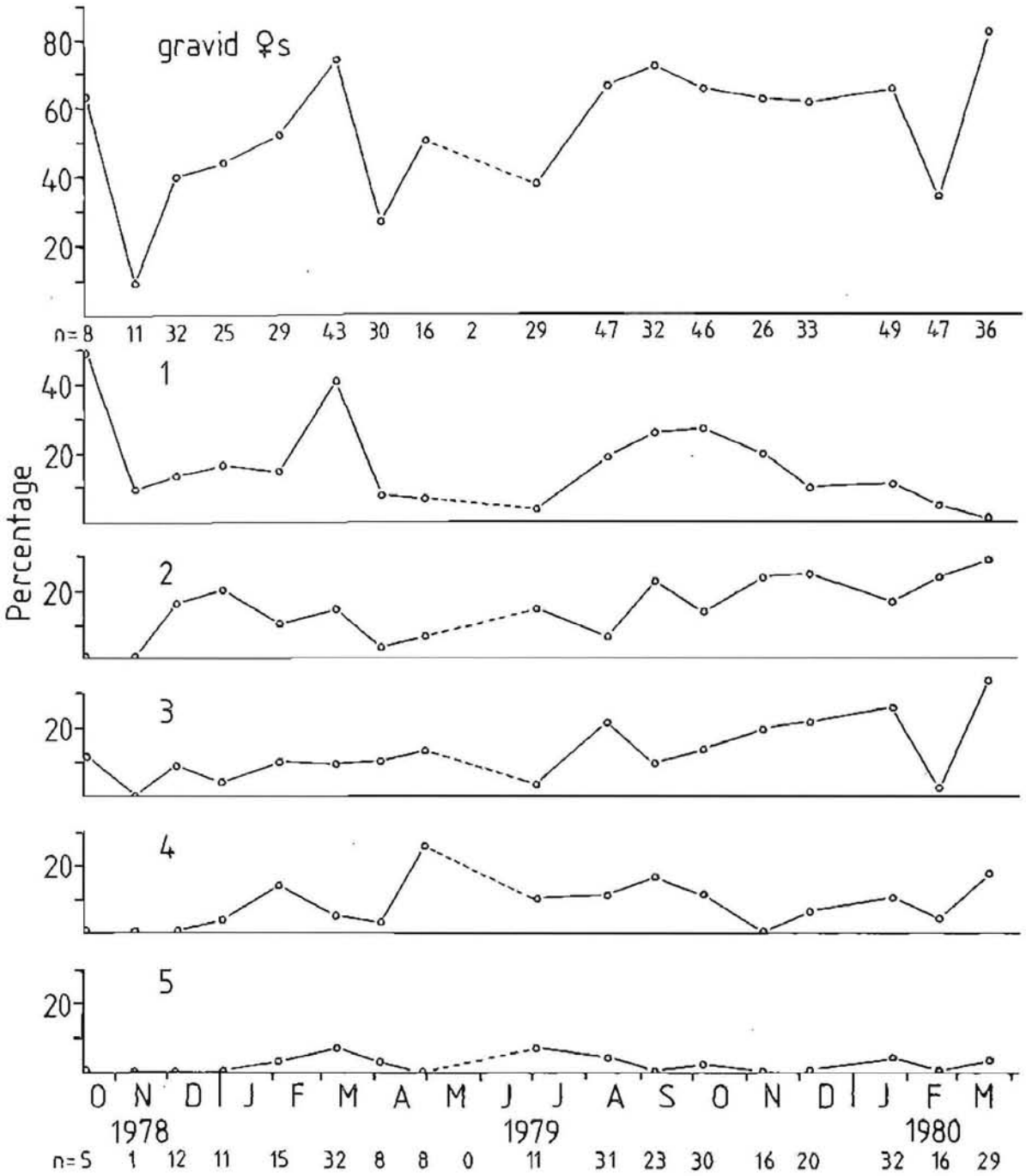

Fig. 6.6 Seasonal changes in the percentage of reproductive females with broods and the percentage of broods at each stage of development.

analysis of seasonal brood composition reflects the overall seasonality described for reproductive females brooding and for recruitment. These data are however, inadequate for determining the duration of embryonic development in the field.

EMBRYONIC DEVELOPMENT

No reliable estimates of embryonic development time were possible from field data but results from 15 gravid females held in the lab. (Appendix 3.1) provided the data in Table 6.4. Thus at 15°C development time fell within the range of 12 - 19+ days with a median duration of 15.5 days. In reality the duration of development probably lies nearer 18 - 19 days. By comparison, embryonic development time at this temperature was 18 days in *Gammarus palustris* (Van Dolah *et al.*, 1975) and about 23.5 days for *Gammarus pulex* (Welton & Clarke, 1980) (Fig. 5.6).

Table 6.4 Estimated duration of embryonic development for *Patuki* at 15°C (see Appendix 3.1).

Development stage	Observed duration (days)	
	Minimum	Maximum
1	2	3+
2	3	4
3	3	4+
4	3	4+
5	1	4

minimum duration : 12 days
maximum duration : 19+ days
median duration : 15.5 days

The mean length of embryos increased significantly between successive developmental stages (Table 6.5) by 21.5% between the first and fourth stages. Similarly the increase in embryo volume between these stages was

Table 6.5 Changes in mean length and volume of embryos during development for *Patuki*.

	Development stage				
	1	2	3	4	5 (head length)
$\bar{x}$ length (mm)	.532	.545	.577	.678	.362
SD	.039	.046	.078	.092	.014
n	219	226	191	124	28
	t = 3.219 p <.01	t = 4.984 p <.001	t = 10.094 p <.001		
	t = 16.836 p <<.001				
$\bar{x}$ volume (mm^3)	.0404	.0438	.0456	.0582	
SD	.0085	.0107	.0143	.0251	
n	55	51	37	26	
	t = 1.802 ns	t = 0.646 ns	t = 2.310 p <.05		
	t = 3.522 p <.001				

30.6%, although the changes between stages 1 - 2 and between 2 - 3 were not statistically significant.

There were marked changes in the mean embryo (stage 1) length from month to month and between seasons (Appendix 3.2, 3.3), but no clear seasonal pattern is apparent (Fig. 6.7). A significant inverse relationship between

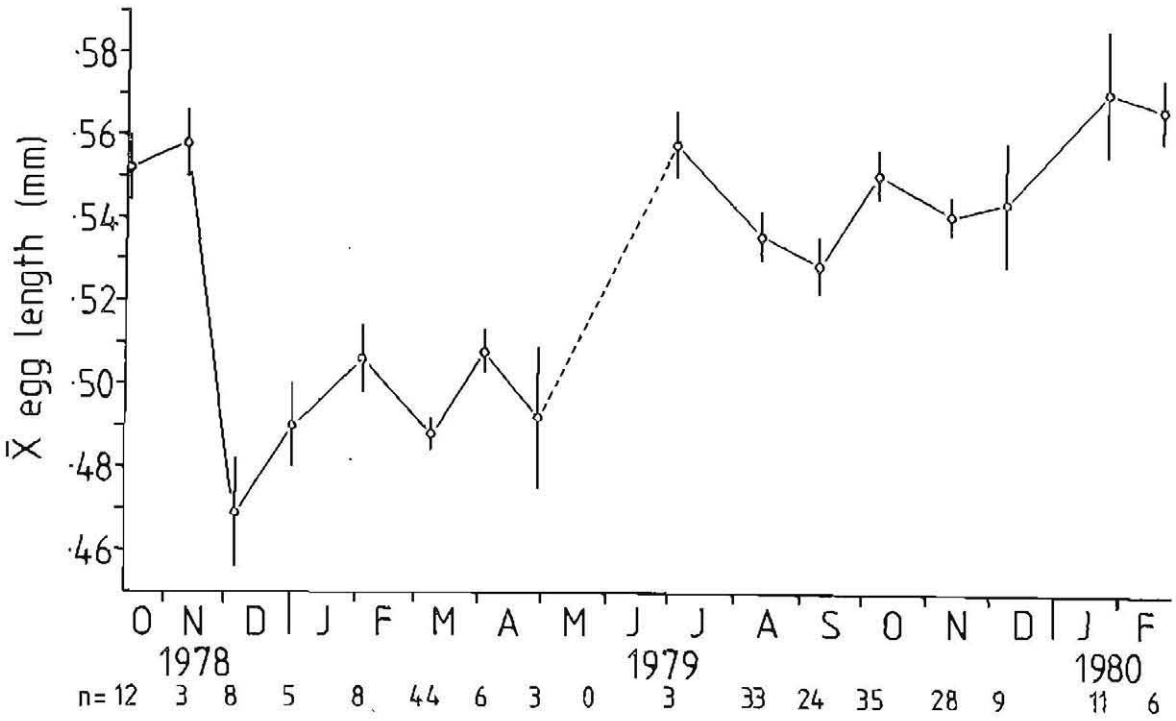

Fig. 6.7 Seasonal changes in the mean (± 1SE) length of stage 1 embryos.

sea water temperature (Fig. 3.4) and mean embryo length for Oct. 1978 - Sept. 1979 was found ($Y = 0.6336 + -0.0085X$, $r = -0.7669$, $p < .01$), but no such relationship existed during the 1979-80 spring and summer. During this latter period larger eggs were produced, possibly as a consequence of greater food availability which, in turn, resulted from the unusually frequent rough seas during Oct. 1979 - Jan. 1980.

BROOD SIZE

The number of embryos per brood ranged between one and 24 with a mean number of 6.673 (SD = 4.536, n = 287). There is a positive relationship between brood size and female size described by the regression equation $Y = -17.969 + 24.568X$ ($r = 0.939$, $p < .001$). The marked seasonal changes in the mean brood size (stage 1 - 2 embryos only) (Fig. 6.8) closely followed changes in the mean size of gravid females, an obvious consequence of the above relationship between the two. As well as varying together, these two parameters show a distinct relationship to sea temperature (Fig. 6.8):

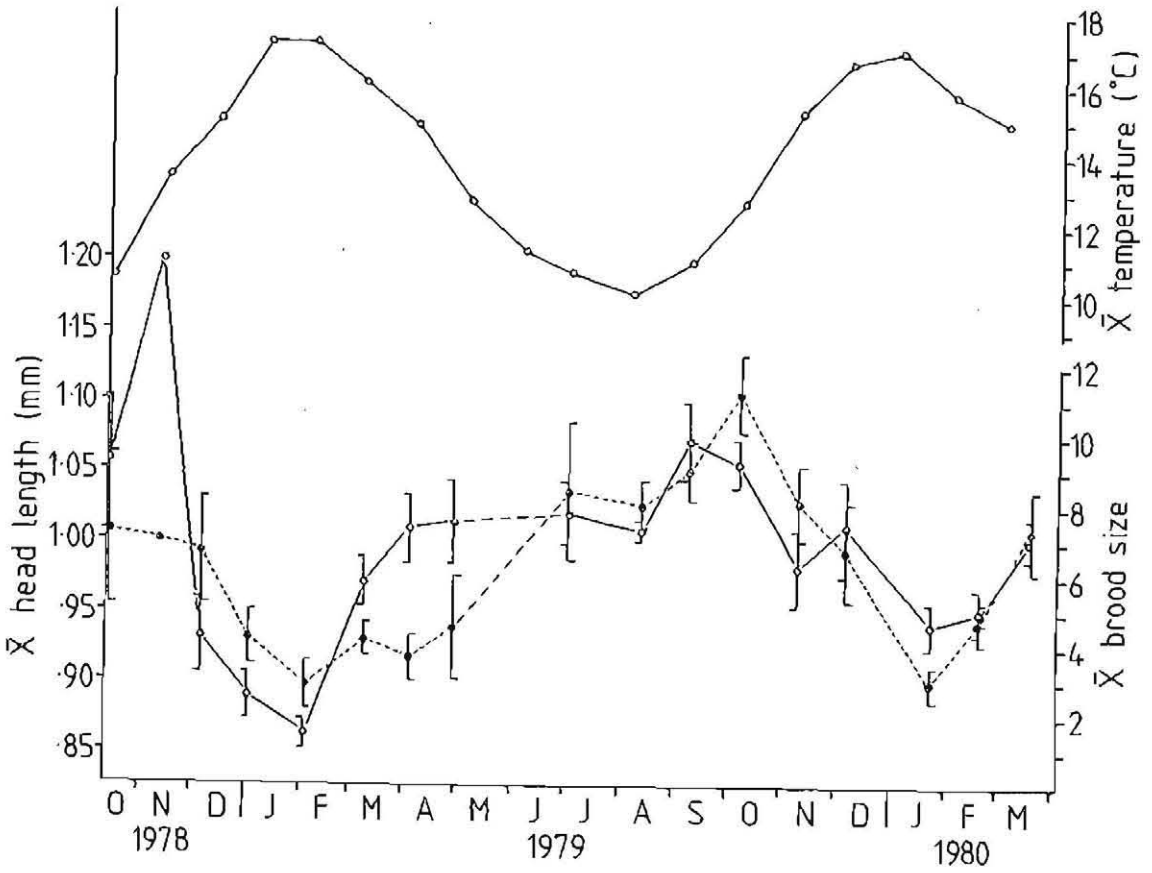

Fig. 6.8 Seasonal changes in mean (± 1SE) brood size (stage 1 - 2 embryos) (broken line), mean (± 1SE) size of gravid females and monthly mean sea temperatures (from Fig. 3.4).

With increasing sea temperature the mean size of females breeding increased with a resultant rise in the mean number of embryos carried. Between Oct. - Dec., the time of early summer storms, larger females of overwintering cohorts disappeared from the population with a resultant decrease in mean brooding-female size and consequent decline in the mean number of embryos per brood. It is notable that the mean brood size (11.22 embryo, SD = 4.89, n = 18) was greater (but not significantly so ($t = 1.636$)) in spring 1979, a particularly stormy spring, compared with spring 1978 (7.25 embryos, SD = 4.27, n = 4). Perhaps an increased food availability as a result of storms allowed greater individual brood sizes. The differences in maximum mean size of gravid females between the two springs probably was apparent only because the Nov. 1978 sample contained only one gravid female.

Table 6.6 Mean brood size at each stage of embryonic development for *Patuki*.

	Development stage				
	1	2	3	4	5
$\bar{x}$	6.192	6.705	7.014	6.978	3.769
SD	4.083	4.337	5.019	4.514	2.279
n	94	88	74	46	13

BROOD MORTALITY

No brood mortality occurred in *Patuki* either between embryonic stages 2 and 4 or between stages 1 and 5 (Table 6.6). Indeed, the largest mean brood size was recorded for broods of stage 3 embryos and again, there was no significant mortality between stages 3 and 4 (0.5%, t = 0.041, n.s.). Although this seems rather unusual among amphipods, especially for a large, active species inhabiting the sediment surface, such a low overall mean brood size precludes the occurrence of appreciable embryo losses. Although data were few, there is some indication that appreciable brood mortality occurred in some seasons and that it may vary with female size (Appendicies 3.4, 3.5).

SEX RATIO

The overall sex ratio observed for *Patuki* was 1.131 males per female, which is essentially 1 to 1 assuming that mortality reduces non-male juvenile abundance between the sizes of male and female recognition. Figure 6.9, a size-frequency plot for juveniles, males and females, confirms that equal numbers of juveniles become males and females, and that the observed difference is attributable to mortality of non-male juveniles. Further, the slightly higher frequency of males larger than 0.500 mm h.l. indicates that the male growth rate slows beyond this size, through either a lower moult frequency or smaller moult increments, or both.

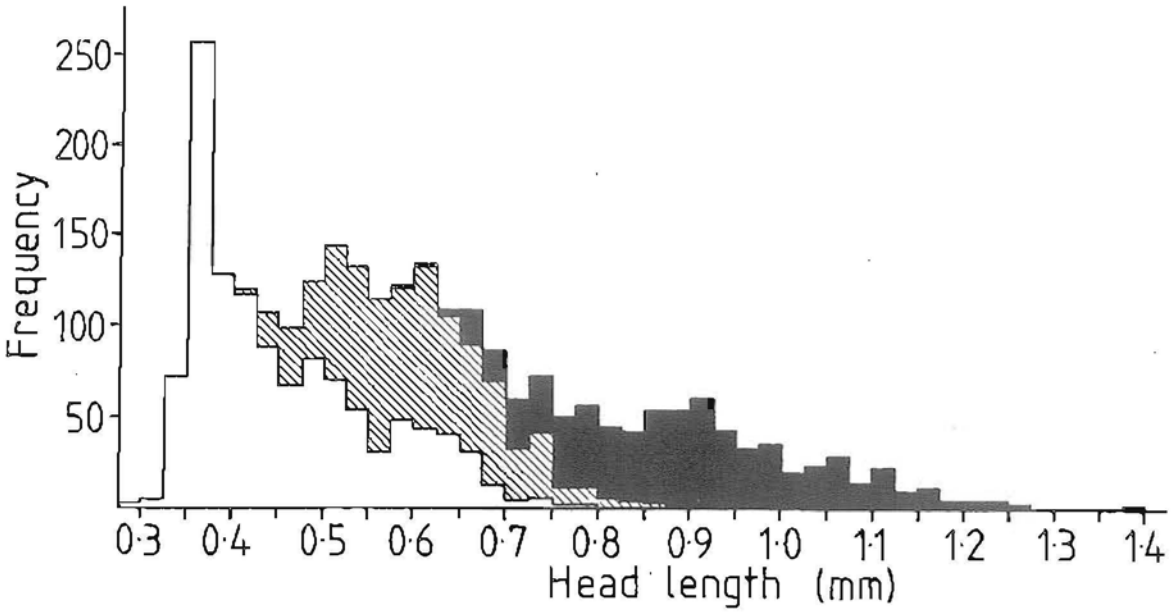

Fig. 6.9 Population size frequency composition Oct. 1978 - Mar. 1980 (unshaded, juveniles; hatched, males; black, females).

Expression of these data (including juveniles) as a male probability curve (Fig. 6.10) is of interest. Within the size range 0.550 - 0.725 mm h.l. more than half of the population was male.. This and the curve's shape qualify the sex ratio as belonging to Wenner's (1972) "intermediate pattern", indicative of partial sex reversal. Here is another example of the deceptiveness of the sex probability curve approach to population sex ratios (see Chapter 5).

Seasonal fluctuations in sex ratio (Fig. 6.11) occur in a pattern resembling changes in population density (Fig. 6.1) and the occurrence of early juveniles (Fig. 6.4). That recruitment of early juveniles should increase the population density is obvious, but the relationship with sex ratio is less so, especially since the changes in sex ratio preceeded the equivalent changes in recruitment by about 30 days. Further, the abundance of males in the population tended to increase with density and to decline to or below parity within a month and before maximum population densities were attained whereas peaks in density persisted longer. As discussed above, breeding is synchronized between cohorts of *Patuki* and the pattern of sex ratio fluctuations indicates that juveniles moult to mature males shortly before the release of new recruits in readiness to copulate with

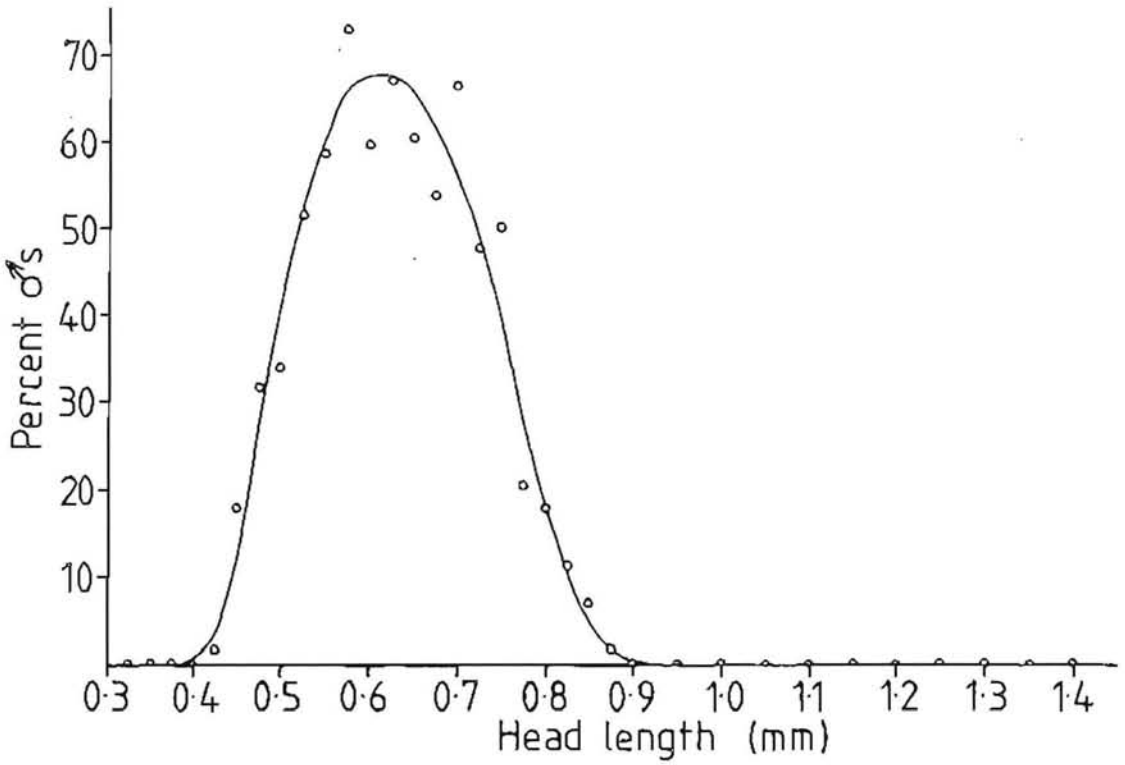

Fig. 6.10 Percentage frequency of males in each size class including unsexable juveniles.

the females which produce the new recruits and eventually produce new broods.

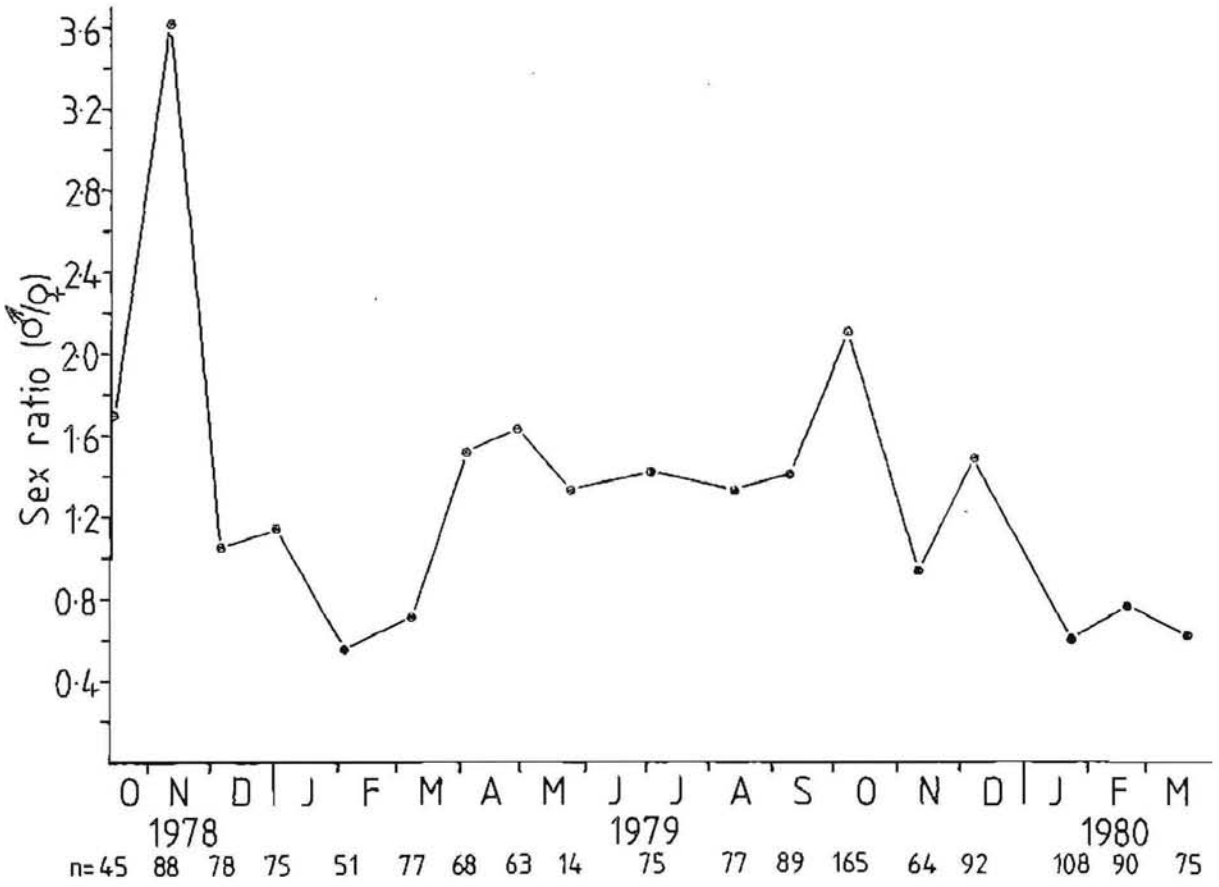

Fig. 6.11 Seasonal changes in sex ratio (♂/♀) of the total population.

CHAPTER 7

POPULATION BIOLOGY OF *METAPHOXUS LITTORALIS*

POPULATION DYNAMICS

POPULATION DENSITY

Densities of this small phoxocephalid ranged between 10 and 405 0.1 m^{-2}, but within each year density variations were less than this range. A regular pattern of seasonal density fluctuations is apparent (Fig. 7.1) with two peaks annually in Nov. - Dec. and Mar. - Apr. During the first summer (1978 - 79) the Nov. - Dec. mean density was just exceeded by the autumn maximum of about 185 0.1 m^{-2}. A very high density of 405 0.1 m^{-2} followed in the next summer (Nov. - Dec. 1979) and the subsequent autumn peak either was not as high (265 0.1 m^{-2}) or it occurred later than in the previous autumn. Thus there was a marked difference in peak mean densities between years. This suggests that when the summer peak is low, a higher autumn peak follows and conversely, high summer peak densities result in lower autumn densities.

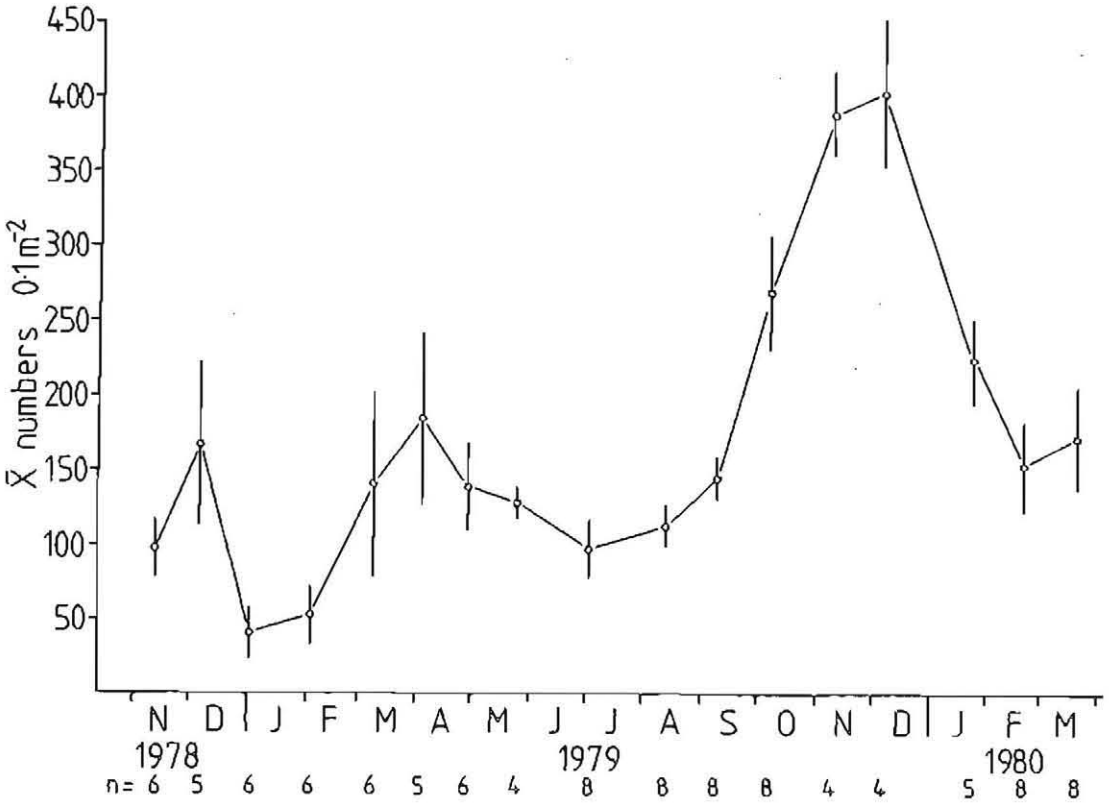

Fig. 7.1 Seasonal changes in mean (± 1SE) density of *Metaphoxus*.

Water temperatures were warmer during spring 1979 than in the previous spring (Fig. 3.4). The mean water temperature reached 11.5°C in late Oct. 1978 whereas it exceeded this temperature about one month earlier the following year. Similarly, the summer maximum temperature was approximately a month earlier in 1979-80 than in 1978-79. Since the summer maximum densities occurred in early Dec. in both years, the population was exposed to warmer temperatures for longer in the 1979-80 summer. Greater reproductive activity and the consequent higher population densities (assuming population size density-independent at observed densities) would be expected.

POPULATION STRUCTURE

At any time the South Bay population of *Metaphoxus* consisted of 6 - 7 cohorts and 10 - 11 new cohorts were produced each year (Fig. 7.2). Both sexes apparently grew at a similar rate but males did not grow as large as females. Males however, matured at an appreciably smaller size (0.450 - 0.475 mm h.l.) and presumably younger age (see Tables 7.1, 7.2) than females (0.551 - 0.650 mm h.l.).

Statistics derived from Fig. 7.2 for males and females of each cohort are presented in Tables 7.1, 7.2. Cohorts are divisable into 2 groups, overwintering (G - L) and summer (M - P), with significant ($p < .05$, Mann-Whitney tests) differences in their ages at various life-history events. Female ages at puberty (Table 7.1) ranged between 55 - 68 days for summer cohorts and 66 - 106 days for overwintering cohorts. Their ages at maturity and their maximum longevities were 85 - 113 days and 191 - 205 days respectively for summer cohorts and 90 - 146 days and 214 - 243 days respectively for winter cohorts. Thus winter cohort females were older at puberty and at maturity, and lived longer than females of summer cohorts. Age at maturity was not however, as discrete as suggested above. Table 7.3 shows that although females may carry broods at 0.501 mm h.l., a substantial proportion of females did not breed until larger than 0.551 mm h.l.

Males of overwintering cohorts (G - L) also were significantly ($p < ,05$, Mann-Whitney tests) older at maturity and lived longer than summer cohort (M - Q) males (Table 7.2). Females of both groups matured later and lived longer than did males of equivalent groups ($p < .05$, Mann-Whitney tests).

RECRUITMENT

Data on cohort longevity and female reproductive activity are summarised

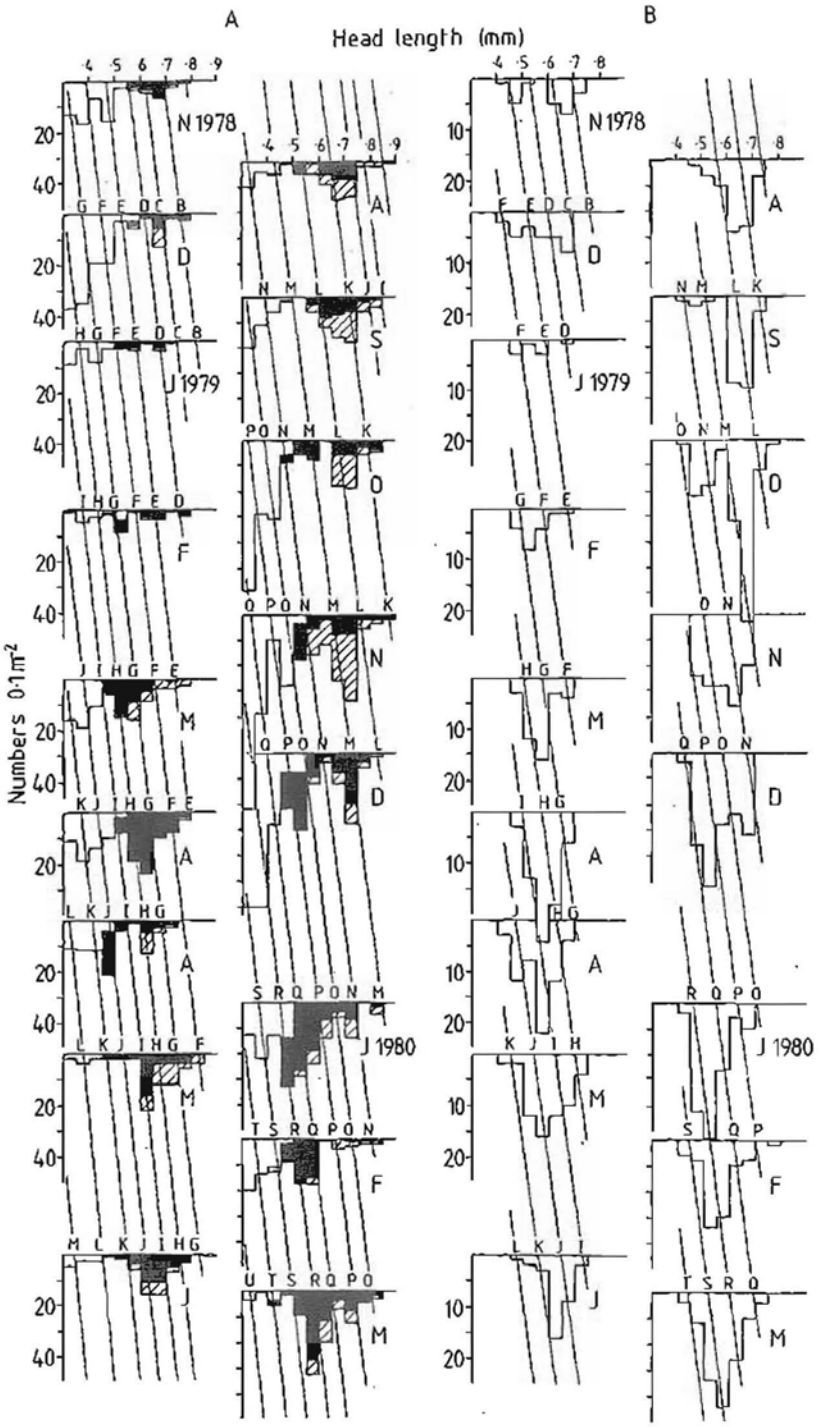

Fig. 7.2 Seasonal changes in the *Metaphoxus* population size-frequency composition for juveniles (unshaded), non-gravid (black) and gravid (hatched) females (A) and for males (B).

Table 7.1 Seasonal occurrence, estimated age at puberty (appearance of oostegites), estimated age at maturity (first brood production) and estimated maximum longevity of female *Metaphoxus* of cohorts G - P (from Fig. 7.2) (over-wintering cohorts bracketed).

Cohort	Seasonal occurrence	Estimated age at puberty (days)	Estimated age at maturity (days)	Estimated maximum longevity (days)
G	Nov.-July	84	117	229
H	Dec.-Aug.	75	90	243
I	Jan.-Aug./Sept.	66	139	233
J	Jan./Feb.-Sept.	81	146	214
K	Mar.-Nov.	73	112	242
L	late Apr.-Dec.	106	120	222
M	July-Jan.	68	113	205
N	Aug.-Feb.	55	89	191
O	Sept.-Mar.	62	89	193
P	Oct.-Mar.+	61	85	165+

Table 7.2 Seasonal occurrence, estimated age at maturity (appearance of penes), and estimated maximum longevity of male *Metaphoxus* of cohorts G - P (from Fig. 7.2) (over-wintering cohorts bracketed).

Cohort	Seasonal occurrence	Estimated age at maturity (days)	Estimated maximum longevity (days)
G	Nov.-late Apr.	84	164
H	Dec.-May	91	164
I	Jan.-July	92	178
J	Jan./Feb.-Aug.	97	203
K	Mar.-Sept.	73	180
L	late Apr.-Oct.	65	161
M	July-Nov.	68	130
N	Aug.-Dec.	41	116
O	Sept.-Feb.	28	164
P	Oct.-Feb./Mar.	47	151
Q	Nov.-Mar.	27	131

Table 7.3 Percent frequency of brooding females in each size class for *Metaphoxus*.

Size class (mm h.l.)	% brooding	n
.451 - .500	0	52
.501 - .550	2.02	99
.551 - .600	25.36	138
.601 - .650	37.01	127
.651 - .700	48.91	137
.701 - .750	52.59	135
.751 - .800	44.19	43
.801 - .850	58.33	24
.851 - .900	66.67	3

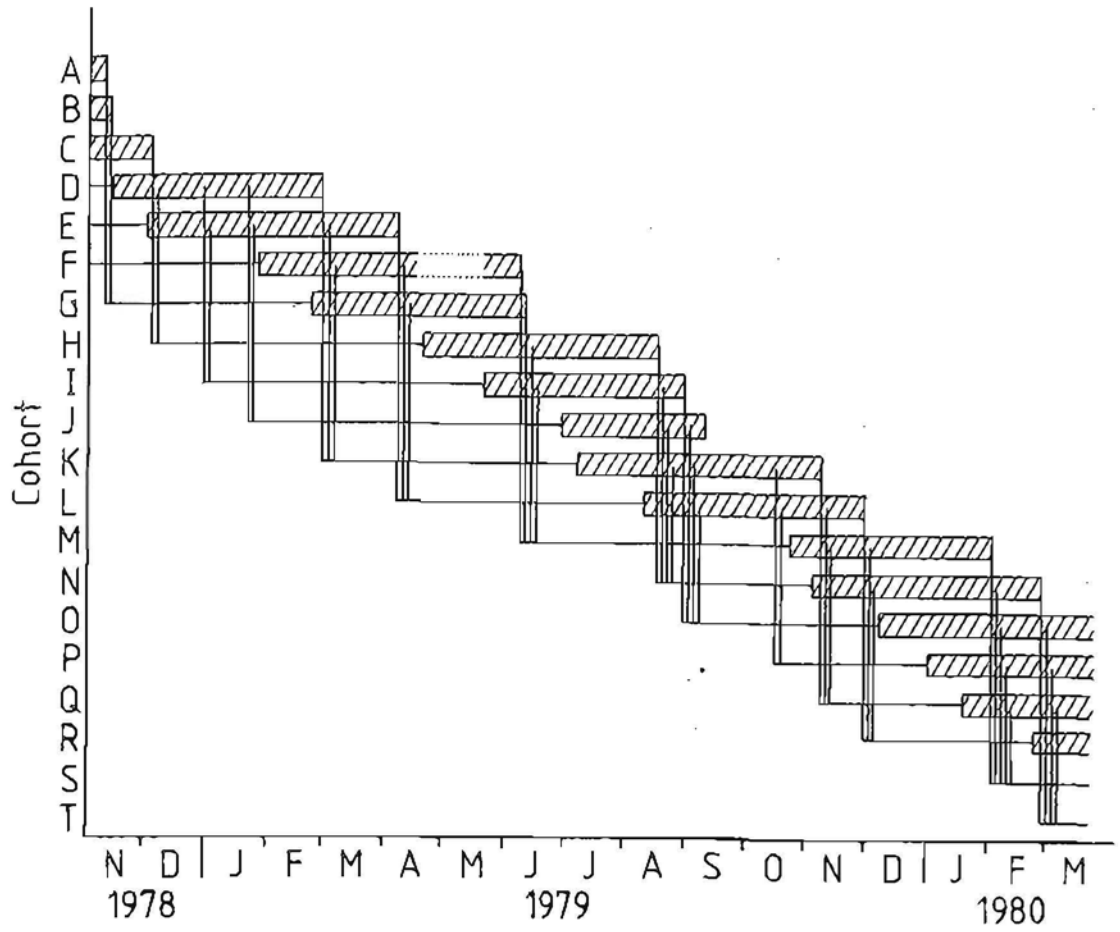

Fig. 7.3 Derivation, seasonal occurrence and egg production of each cohort of *Metaphoxus* (shaded bars, gravid females).

in Fig. 7.3 and the probable origins of each new cohort are indicated. Gravid females were present in all months and recruitment occurred irregularly throughout the year. A new cohort was produced approximately monthly during both summers except in Dec. 1979 - Jan. 1980, a period of frequent rough seas (Fig. 3.3). Recruitment was less frequent and quite irregular during the six months between Apr. and Sept.; only four new cohorts originated and two of these in close succession in mid Aug. - early Sept. Thus it seems that new cohorts are produced at about monthly intervals when sea temperatures are above 14.0°C, but this pattern may be disrupted by stormy seas.

The seasonal density of new recruits in the population (Fig. 7.4) does not reflect the pattern of cohort appearance, indicating a marked seasonal bias in breeding success and/or survival of juveniles beyond recruitment.

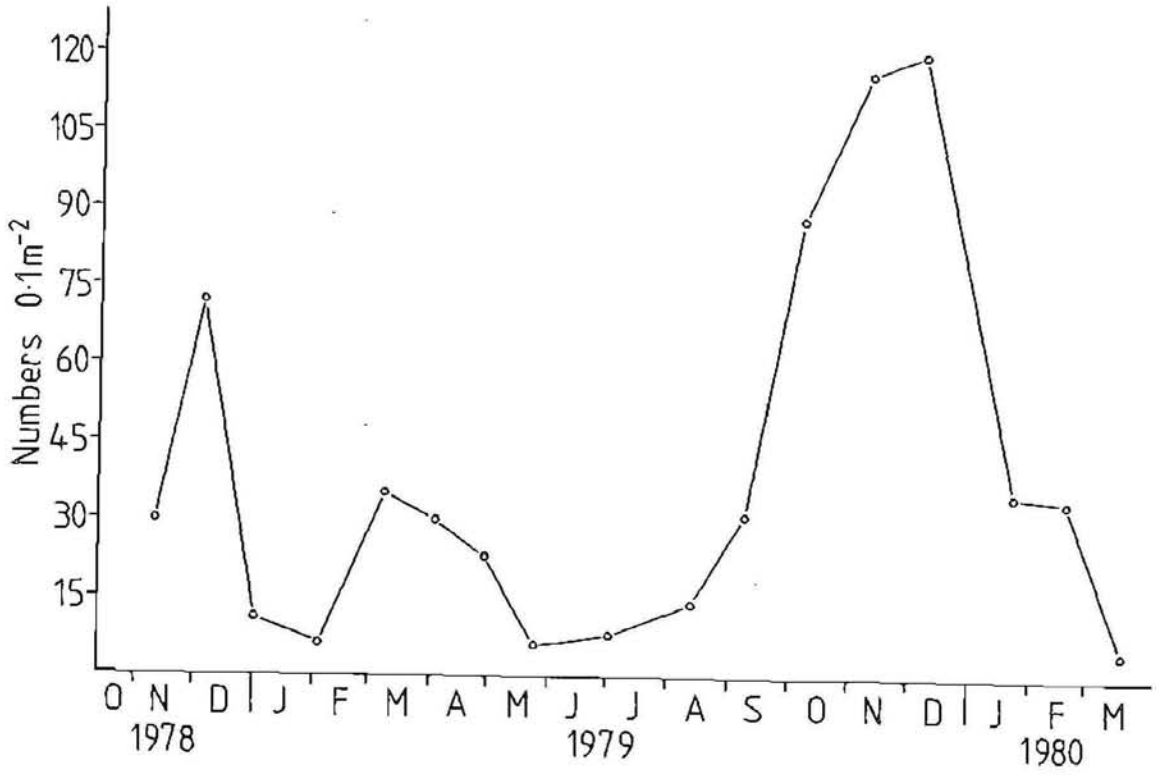

Fig. 7.4 Seasonal changes in density of juvenile *Metaphoxus*.

Comparison of Fig. 7.4 with Fig. 7.1 shows that recruitment and mortality (and/or emigration) are the principal factors determining the total population density. Immigration must be of negligable importance however, because total density closely follows the pattern of recruit density.

Recruits to a cohort may originate from 2 - 4 parental cohorts suggesting some breeding synchrony between cohorts. A series of regression analyses failed to detect any relationship between breeding activity (percent gravid females with new broods, percent early juveniles in the population) and either lunar periodicity or the occurrence of storms.

REPRODUCTION

OCCURRENCE OF BREEDING

The percentage of reproductive (h.l. >0.575 mm) females brooding was remarkably similar from season to season (Fig. 7.5); only once in Nov. 1979

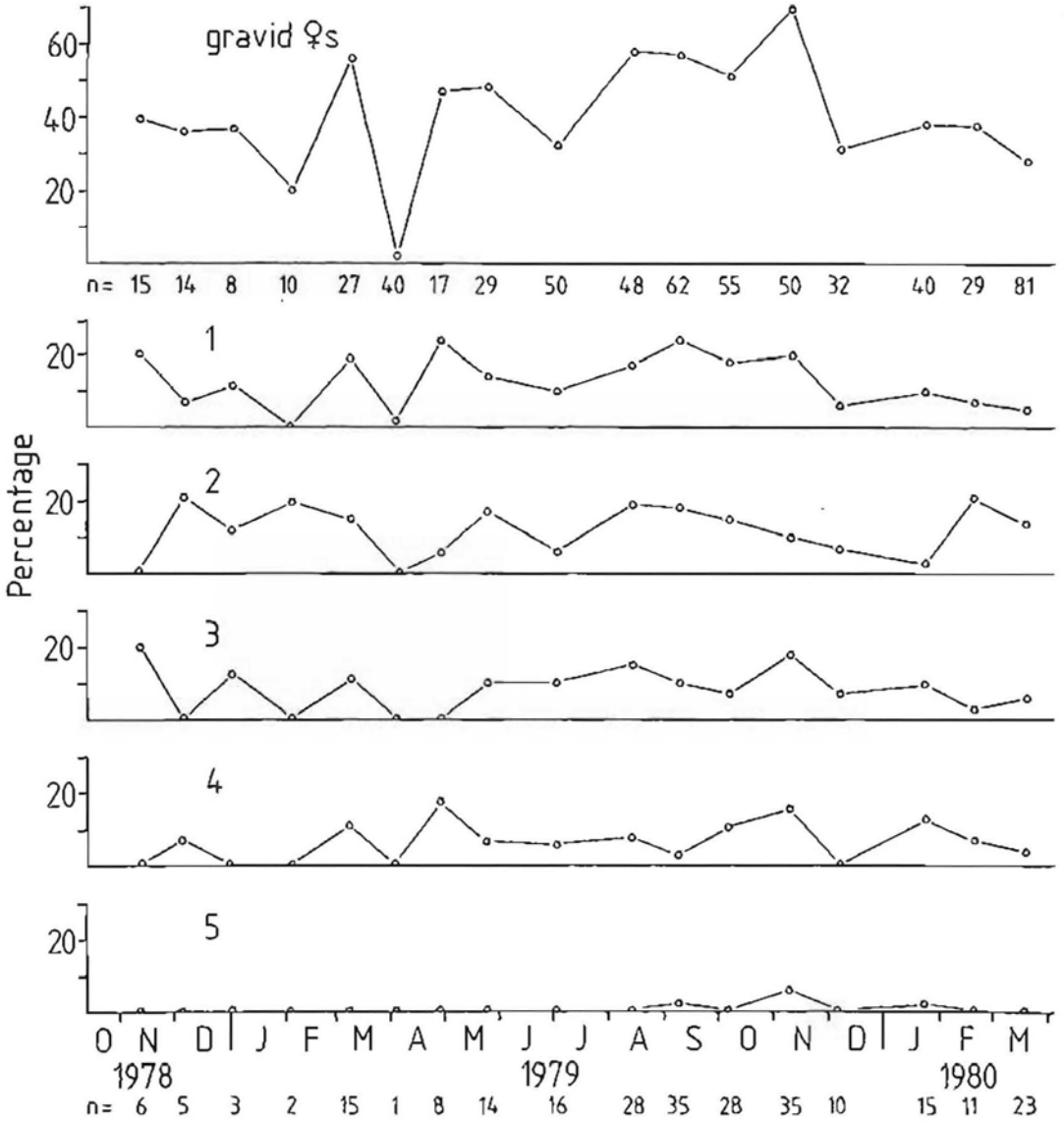

Fig. 7.5 Seasonal changes in the percentage of reproductive females (h.l. >0.575 mm) with broods and the percentage of broods at each stage of development.

were more than 60% carrying broods and only twice (Feb. and early Apr. 1979) were fewer than 30% brooding. These data and those in Table 7.3 show that reproductive activity of the population as a whole must be non-synchronous with a significant proportion of reproductive females always about to produce broods. Further, there were no marked peaks in the occurrence of broods at any development stage (Fig. 7.5), but instead broods were fairly evenly spread among stages 1 - 4 at all times.

EMBRYONIC DEVELOPMENT

Field data (Fig. 7.5) provided no indication of the duration of embryonic development but the durations of each developmental stage were estimated by checking 12 gravid females held at 15°C in the lab. (Appendix 4.1). The maximum and minimum durations for each stage (Table 7.4) derived from the lab. data give a total development time of between 13 and 26 days and the true duration probably lies within the lower half of this range, perhaps near 15 - 16 days. This compares favourably with published durations of embryonic development times (Steele & Steele, 1973; Van Dolah *et al.*, 1975; Welton & Clarke, 1980), especially when the relationship between duration of development and egg size (Steele & Steele, 1973, 1975c) is considered.

Table 7.4 Estimated duration of embryonic development for *Metaphoxus* at 15°C (see Appendix 4.1).

Development stage	Observed duration (days) minimum	maximum
1	1	4
2	3	6
3	3	6+
4	4	5
5	2	5

minimum duration: 13 days
maximum duration: 26 days
median duration: 19.5 days

Undifferentiated eggs (early stage 1) were about 0.375 mm greatest length. As development proceeded embryos increased in size significantly (Table 7.5); embryo length increased by 31.97% between stages 1 and 4 and volume increased by 17.32% from stage 1 to 3. The observed volume increase of 62.13% between

Table 7.5 Changes in mean length and volume of embryos during development for *Metaphoxus*.

	Development stage			
	1	2	3	4
$\bar{x}$ length (mm)	.3825	.3759	.4126	.5048
SD	.0287	.0472	.0644	.0651
n	209	167	145	79
	t = 1.5877	t = 5.6668	t = 10.1664	
	n.s.	p <.001	p .001	
	t = 16.1163			
	p <<.001			
$\bar{x}$ volume (mm^3)	.01611	.01469	.01890	.03042
SD	.00249	.00463	.00538	.01339
n	71	50	38	11
	t = 1.9767	t = 3.8586	t = 2.7890	
	p ∿.05	p <.001	p <.01	
	t = 3.5351			
	p <.001			

stages 3 and 4 seems unreasonably high and the wide variation in stage 4 embryo size (SD = 0.0134) indicates some error, perhaps resulting from alteration of stage 4 embryo size with preservation.

Egg lengths varied slightly from month to month between 0.368 and 0.410 mm (Appendix 4.2) and the difference between successive months was significant only for Nov. - Dec. 1978. A seasonal analysis of egg lengths (Appendix 4.3) showed that eggs were significantly ($p < .001$) smaller ($\bar{x}$ = 0.360 mm, SD = 0.044, n = 17) in the 1978 - 79 summer (Dec. - Feb.) than in all subsequent seasons (range $\bar{x}$ = 0.373 - 0.398) including the following summer. As noted above, spring 1978 was not as warm as in the following year and this may underlie the observed smaller egg sizes which, in turn, possibly resulted in the lower recruitment and overall produced population density seen during the 1978 - 79 summer. No relationship between monthly mean egg size and sea temperature was evident.

BROOD SIZE

Female *Metaphoxus* brood between one and nine embryos and the mean brood size was 2.705 (SD = 1.695, n = 173). Numbers of eggs brooded increased linearly with female size following the relationship $Y = -10.779 + 19.114X$ ($r = 0.963$, $p < .01$). There was a marked seasonal change in monthly mean brood size (stage 1 - 2 embryos only) (Fig. 7.6). Broods consisted of fewer embryos early in the year (Feb. - Mar. to July) but increased to maximum mean sizes between Oct. and Jan. The summer period of larger brood sizes was however interrupted briefly in Nov. or Dec. when an appreciably lower mean number of embryos was carried. Figure 7.6 shows that the changes in mean brood size are largely a result of changes in the mean size of females brooding; both show a winter trough, a spring increase to the summer peak which is broken by a brief decline, and a general decline in autumn. The brief, midsummer decrease in mean brood size and in the mean size of brooding females occurred in Nov. when the percentage of reproductive females peaked at 70% (Fig. 7.5) and just prior to the maximum total population density (Fig. 7.1), suggesting perhaps that for a brief period (Oct. - early Nov.) food became scarce and limited egg production. Subsequently, mean brood size and mean brooding female size increased coincident with a sharp decline in the percentage of adult females brooding.

It is notable that between Nov. and Mar. the mean brood size was consistently higher during 1979 - 80 (Fig. 7.5) and, although not so obvious,

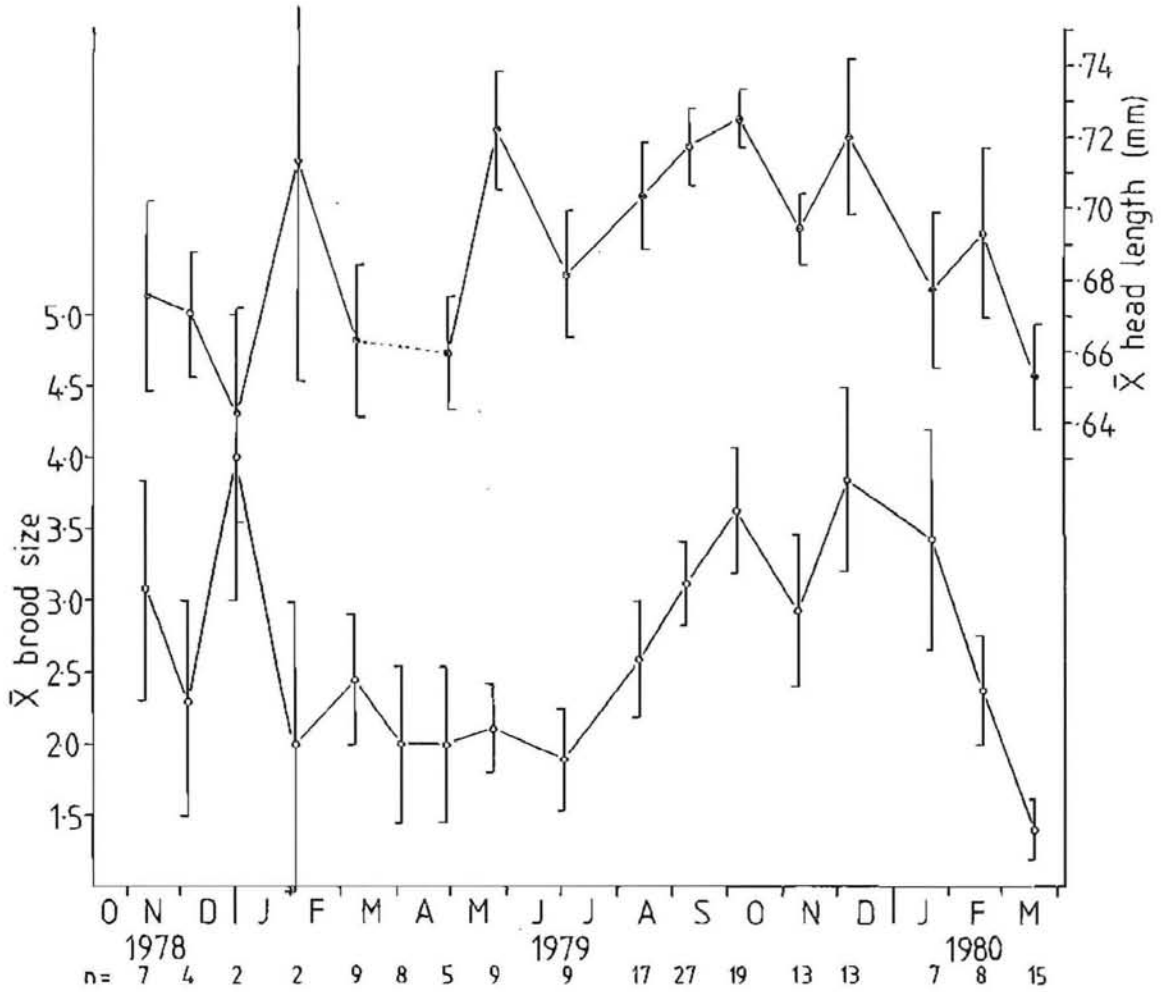

Fig. 7.6 Seasonal changes in the mean (± 1SE) brood size (stage 1 - 2 embryos) and mean (± 1SE) size of gravid females.

the same is true for the mean size of brooding females. Further, the total population densities (Fig. 7.1) and the densities of recruits (Fig. 7.4) for this period also were markedly higher in 1979 - 80 than in the previous summer. Thus, females were bigger and produced more offspring that eventually entered the population and the total population was larger in 1979 - 80 than in 1978 -79. Earlier warmer temperatures in the second summer explain only part of this difference. Biotic factors (reduced predation pressure, reduced densities of competing species, etc.) along with a greater abundance of available food as a direct or indirect consequence of the more frequent stormy

Table 7.6 Mean size of broods at each stage of embryonic development for *Metaphoxus*.

	Development stage				
	1	2	3	4	5
$\bar{x}$	2.872	2.622	2.836	1.791	2.000
SD	1.827	1.568	1.551	1.103	1.528
n	94	74	61	43	7
		t = 3.350 p <.001		t = 0.348 n.s.	
			t = 1.368 n.s.		
			t = 4.037 p <.001		
		t = 2.363 p <.05			

seas (Fig. 3.3) in 1979 - 80 possibly contributed to this difference also.

BROOD MORTALITY

Table 7.6 presents the mean brood size at each developmental stage for all gravid females. In this case brood mortality was calculated between the first and fifth stages because stage 1 broods contained most embryos and stage 5 broods were larger than stage 4 broods. *Metaphoxus* thus suffers surprisingly high (30.4%) brood mortality for a small species producing so few eggs per brood. Females must then produce at least two broods per lifetime on average to compensate for the few eggs per brood and their high

mortality. Additional reproductive mechanisms employed to maintain the population include breeding throughout the year and nonsynchrony of breeding with a high proportion of the female population producing new broods.

There is some indication of seasonal differences in brood mortality and that different sized females loose different proportions of their broods (Appendicies 4.4, 4.5), but data were inadequate for analysis of these questions.

SEX RATIO

The overall sex ratio (σ/φ) of 0.820 for *Metaphoxus* deviated significantly (χ^2 = 13.681, p <.001) from parity emphasizing the abundance of females in the population. This is obvious from Fig. 7.7A which shows the strong predominance of females in size classes greater than 0.725 mm h.l. It is not possible to determine the sex ratio at the time of juvenile release in these amphipods, and estimates of the sex ratio at puberty or maturity are unreliable because males mature at a smaller size and when younger than females. Instead, the sex ratio for size classes between 0.525 mm h.l. (the smallest size class containing relatively few juveniles) and 0.675 mm h.l. (the size class preceeding the decline in male abundance (Fig. 7.7A) and obvious predominance of females) was 1.118 or essentially 1 to 1 (χ^2 = 2.843, n.s.). Thus the population sex ratio is considered to be at parity. In size classes greater than 0.675 mm h.l. however, mortality selectively removes males from the population at a smaller size and more rapidly than females so that in these larger size classes the sex ratio (0.168) is overwhelmingly in favour of females.

Presentation of these data as a male probability curve (Fig. 7.7B) adds nothing to the histogram and the above discussion. It does, however, simplify expression of the changes in sex ratio with size but the impact of female survival to a larger size is not apparent.

Seasonal variations in the sex ratio show no pattern, are wide and erratic, and could not be correlated with any factor or population statistic (Fig. 7.8). There was however, some tendency for the sex ratio (proportion of males) to increase as the percentage of adult females brooding (Fig. 7.5) declined.

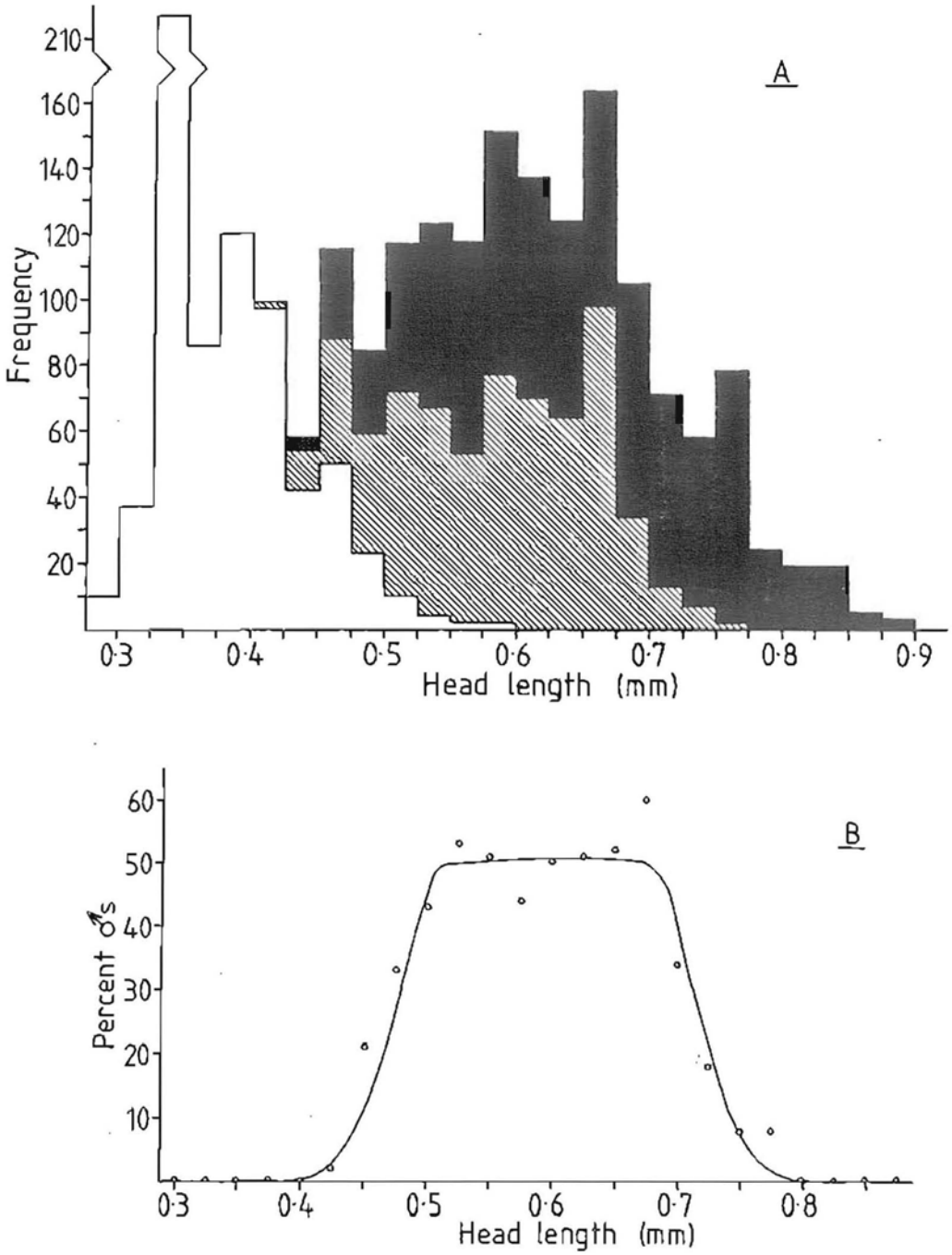

Fig. 7.7 Population size-frequency composition Oct. 1978 - Mar. 1980(A) (unshaded, juveniles; hatched, males; black, females), percentage frequency of males in each size class excluding unsexable juveniles (B).

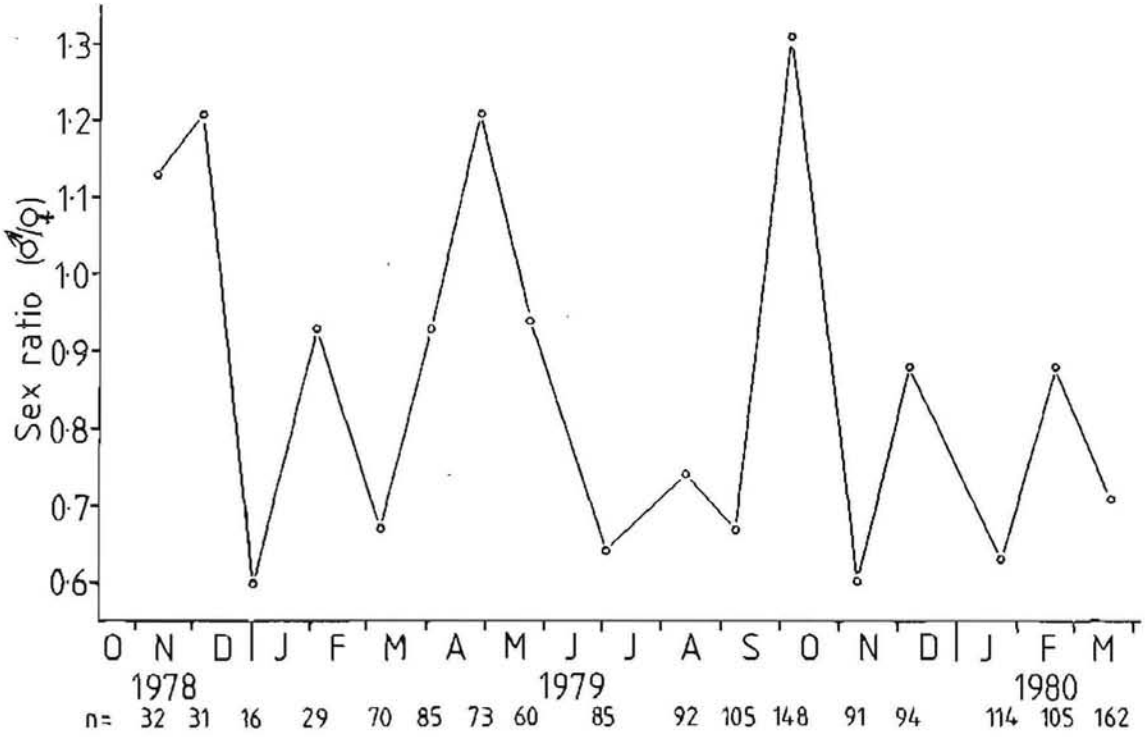

Fig. 7.8 Seasonal changes in sex ratio ($^{\sigma}/_{\varphi}$) of the total population.

CHAPTER 8

POPULATION BIOLOGY OF *PARAPHOXUS AUSTRALIS*

POPULATION DYNAMICS

POPULATION DENSITY

The seasonal population density fluctuations of *Paraphoxus* (Fig. 8.1) are quite remarkable in ranging between about 12 and 440 0.1 m^{-2} in one year. Densities followed the expected pattern of a spring increase from about Aug. to a summer maximum between Dec. - Mar. and thereafter a steep decline to winter minima by Apr. - May. Between years the summer peak was quite variable in height and in form. In 1978 - 79 there was a marked decline in density in Nov. just before the Dec. maximum of almost 440 0.1 m^{-2} and another immediately after in Jan. - Feb. before a further, lesser peak in Mar. The low winter densities did not occur until May. Next summer saw a steady increase in density from Oct. until the maximum of 183 0.1 m^{-2} in Mar. after which densities plummeted to the winter minimum by Apr. Insufficient information is available to explain these summer density differences but it is conceivable that food was scarce as a result of the calm winter and limited reproductive activity (Fig. 3.3). In addition the stormy periods during spring and summer may have increased the mortality of recruits.

A small midwinter increase in density occurred from May to July in both years and although not great in magnitude, its recurrence at the same time each year implies some significance. Assuming that the population size is density-dependent and that the autumn decline is a response to this, then the midwinter increase may occur once the population has declined beyond its density-limiting size for that time. That is, during the initial stages of the autumn decline the population is density-dependent but the final stages are an overshoot and not density-dependent. During May - June the population was free of density constraints and increased beyond the habitat carrying capacity by July. Thereafter ensued another decline mediated by density-dependent factors.

It is notable that the population density commenced its spring increase just after the sea temperature minima in Aug. during both years. This further indicates that the population was largely density-limited because, with warmer temperatures, an increase in habitat productivity and food availability

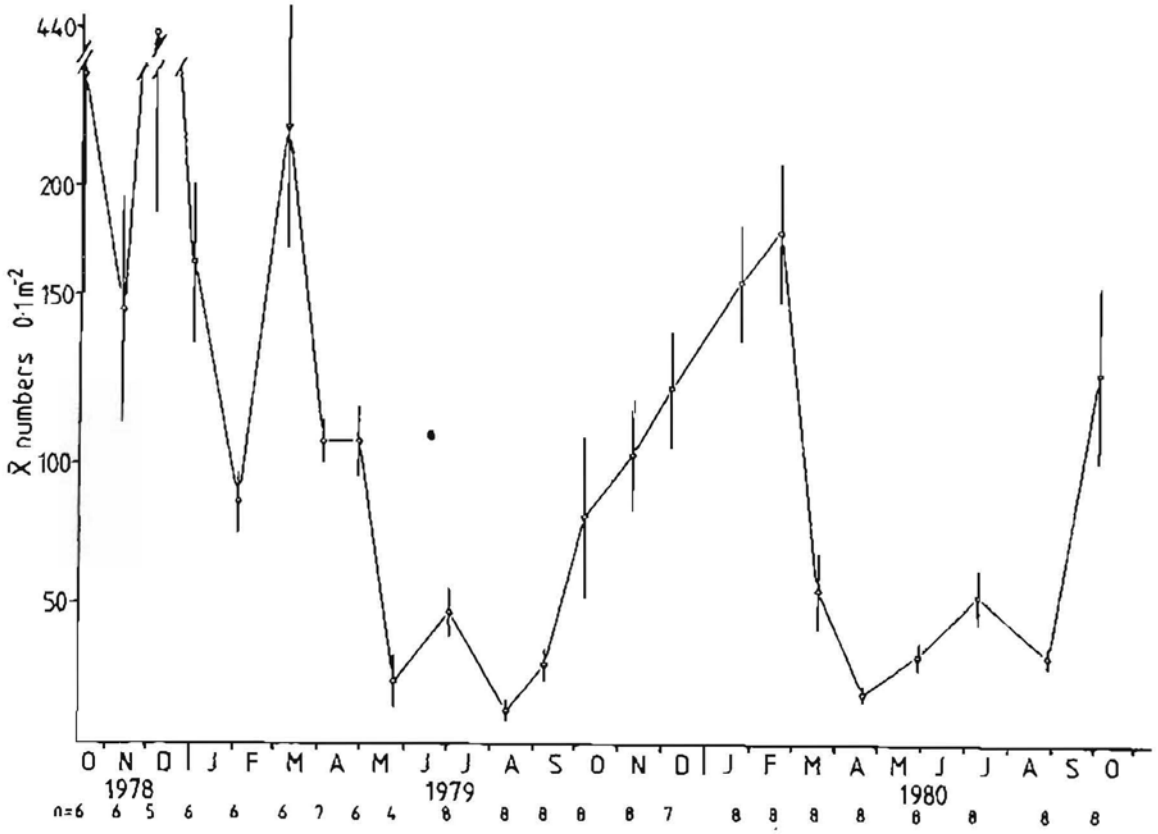

Fig. 8.1 Seasonal changes in mean (± 1SE) density of *Paraphoxus*.

is likely.

POPULATION STRUCTURE

The *Paraphoxus* population varied considerably in structure between months and between years. It consisted of five to nine cohorts at any time and seven and eight cohorts were produced annually in 1978 - 79 and 1979 - 80 respectively (Figs. 8.2, 8.3).

Males (Fig. 8.3) were distinguishable at a smaller size than females (Fig. 8.2) and did not grow as large as females. Presumably males matured at a smaller size and younger age than females. Field data (Figs. 8.2, 8.3) indicate that each sex grew at a similar rate of about 0.1013 mm per 30 days. Measurements of 15 individuals in the lab. (Appendix 5.1) yielded a mean growth rate of 0.0651 mm per 30 days (SD = 0.0357), independent of season ($t = 0.01710$, dfs = 13, n.s.), which indicates that the above (Figs. 8.2, 8.3) interpretation of population structure is not unreasonable.

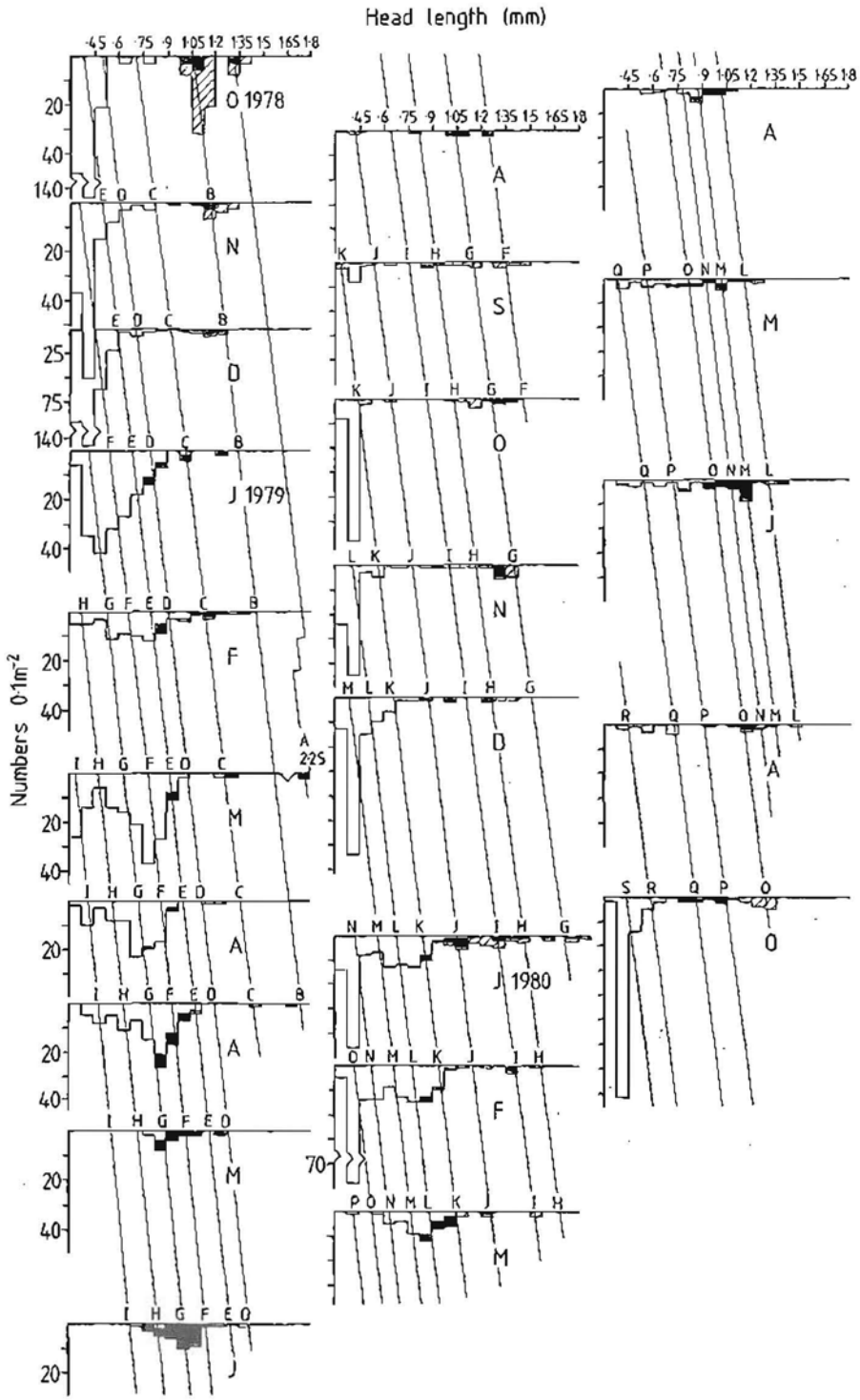

Fig. 8.2 Monthly changes in the *Paraphoxus* population size-frequency composition for juveniles (unshaded), non-gravid (black) and gravid (hatched) females.

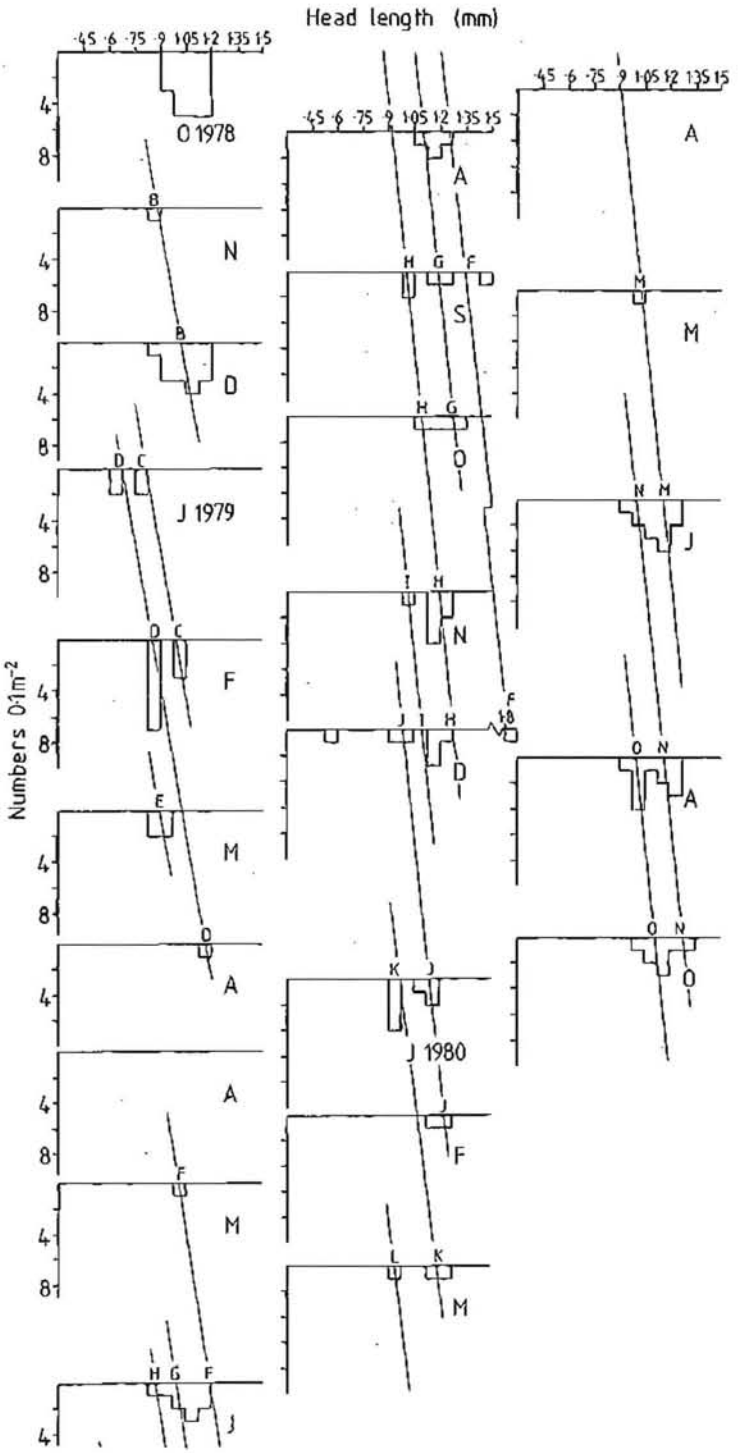

Fig. 8.3 Monthly changes in the *Paraphoxus* population size-frequency composition for males.

Female *Paraphoxus* lived for up to 434 days, reached puberty and developed recognizable oostegite buds when 0.750 - 0.950 mm h.l. at about 100 - 180 days old and carried their first brood at 191 - 242 days (Table 8.1). Males possessed penes when about 0.850 mm h.l. at 131-242 days old and thus were presumed sexually mature (Table 8.2).

Cohorts were divisable into two groups (Table 8.1, 8.2), summer-autumn breeders and winter-spring breeders, approximately equivalent to the summer and the over-wintering cohorts respectively of shorter-lived species. Females of both cohort groups attained puberty at about the same age, but both males and females of winter-spring breeding cohorts matured later and lived longer than summer-autumn breeding cohorts (Mann-Whitney tests, $p < .05$).

As with other species, females did not all mature at the same size (and age) as shown in Table 8.3. About 40% of females carried broods when about 1.075 - 1.125 mm h.l., but in subsequent analyses all females larger than 1.000 mm h.l., the size of smallest females brooding, are considered mature.

REPRODUCTION

BREEDING AND RECRUITMENT

Figure 8.4 summarises much of the above information and for each cohort it shows the possible parental cohorts. Each new cohort arose from at least one parental cohort but close examination revealed no relationship between breeding activity and lunar periodicity or the occurrence of storms.

At almost any time gravid females in the population belonged to two and occasionally up to four different cohorts. The exception to this occurred between Mar. and July 1979; in late Mar. the four oldest cohorts (H - K) containing all mature females, disappeared so that the population consisted of four immature cohorts (L - O) and one newly recruited cohort (P). This occurred during the very sharp autumn decline in population density (Fig. 8.1), possibly in response to limited food availability. Further, although a new cohort was added at this time from perhaps four parental cohorts (Fig. 8.4), it consisted of very few individuals (Fig. 8.5).

Despite the irregular addition of new cohorts, there exists a well-defined, annual pattern of recruitment (Fig. 8.5) which, as expected, is similar to the annual population density pattern (Fig. 8.1). Significant recruitment was

Table 8.1 Seasonal occurrence, estimated age at puberty (appearance of oostegites), estimated age at maturity (first brood production), and estimated maximum longevity of female *Paraphoxus* cohorts E - Q (spring breeders bracketed).

Cohort	Seasonal occurrence	Estimated age at puberty (days)	Estimated age at maturity (days) & month of first breeding	Estimated maximum longevity (days)
E	Oct.-July/Aug.	114	194 late Apr.	280
F	Nov.-Jan.	143	229 July	434
G	Jan.-Jan.	113	233 Aug./Sept.	383
H	Feb.-Feb.	145	241 Oct.	377
I	Mar.-Mar.	180	242 Nov.	373
J	Aug.-Mar.	116	164 Jan.	220
K	Sept.-Mar./Apr.	137	193 Mar.	209
L	Nov.-Aug.	116	202 May	293
M	Dec.-Aug.Oct.+	120	216 July	284+
N	Jan.-Oct.+	127	218 Aug.	253+
O	Feb.-Oct.+	100	191 Aug.	226+
P	Mar.-Oct.+	112	197 Oct.	197+
Q	May-Oct.+	126		

Table 8.2 Seasonal occurrence, estimated age at maturity (appearance of penes), and estimated maximum longevity of male *Paraphoxus* cohorts E - O (spring breeders bracketed).

Cohort	Seasonal occurrence	Estimated age at maturity (days)	Estimated maximum longevity (days)
E	Oct.-July	147	259
F	Nov.-Dec.	190	386
G	Jan.-Oct.	158	273
H	Feb.-Dec.	145	302
I	Mar.-Dec./Jan.	242	293
J	Aug.-Feb.	164	239
K	Sept.-Mar.	137	193
L	Nov.-?Apr.	131	163
M	Dec.-July	175	216
N	Jan.-Oct.	168	253
O	Feb.-Oct.+	191	226+

Table 8.3 Percent frequency of different sized *Paraphoxus* females brooding embryos.

Female size class (h.l., mm)	% brooding	n
.700 - .750	0	2
.775 - .825	0	11
.850 - .900	0	19
.925 - .975	0	38
1.000 - 1.050	11.86	59
1.075 - 1.125	39.62	53
1.150 - 1.200	51.06	47
1.225 - 1.275	55.88	34
1.300 - 1.350	67.65	34
1.375 - 1.425	70.00	20
1.450 - 1.500	83.33	6
1.525 - 1.575	100.00	3
1.600 - 1.650	50.00	2
1.675 - 1.725	0	1
1.750 - 1.800	-	0
1.825 - 1.875	-	0
1.900 - 1.950	-	0
1.975 - 2.025	-	0
2.050 - 2.100	50.00	2
2.125 - 2.175	100.00	1
2.200 - 2.500	0	1

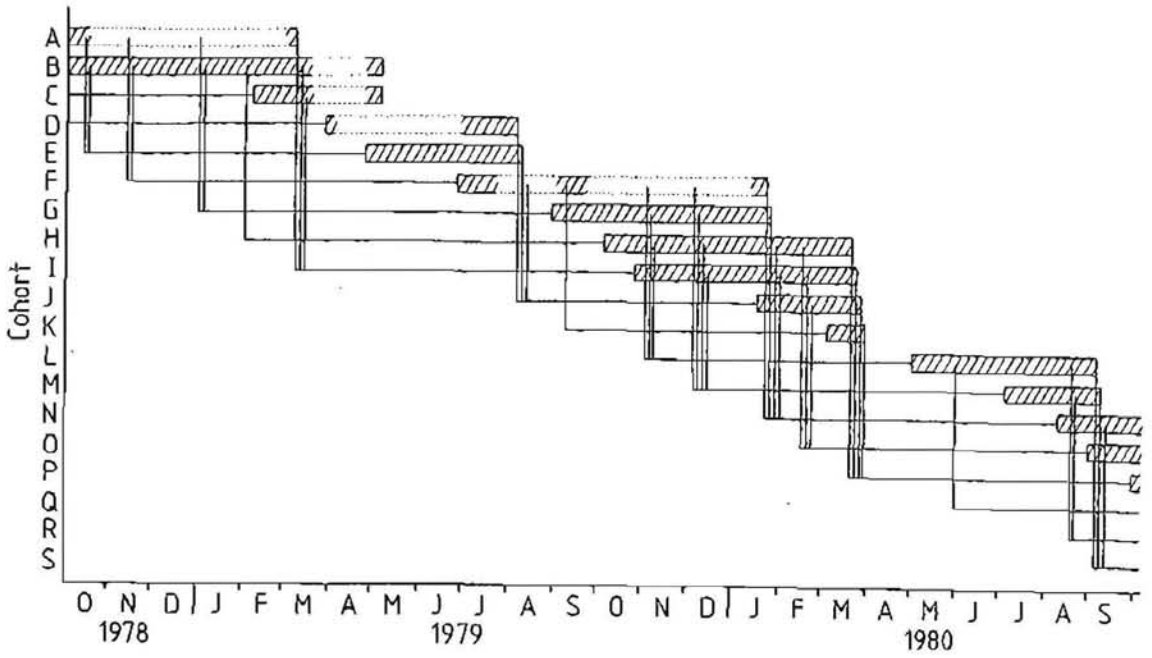

Fig. 8.4 Derivation, seasonal occurrence and egg production of each cohort of *Paraphoxus* (shaded bars, gravid females; broken lines, minor contributions).

confined to the warmer months with the most recruits added during the period Sept. - Oct. to Feb. - Mar. Almost no recruitment occurred between Apr. and Aug. but there was a consistent and appreciable increase in population density in July (Fig. 8.1) indicating significant immigration to the population during winter. There is some suggestion of immigration into the population in the 1979 autumn also, for the Feb. population density plus the Mar. recruits (86 + 40 = 126 individuals 0.1 m^{-2}) is far short of the Mar. population density (221 individuals 0.1 m^{-2}).

Between years the numbers of recruits entering the population varied markedly and this variation is reflected by the annual variations in total density. As discussed above, brood production and recruitment were less successful during 1979 - 80 probably through the direct and indirect effects of warmer sea temperatures and more frequent rough seas.

Although there were wide month-to-month variations in the proportion of adult (h.l. >1.00 mm) females brooding (Fig. 8.6), a summer period of greater brood frequency is clearly evident. This spanned the period Aug. - Sept. to

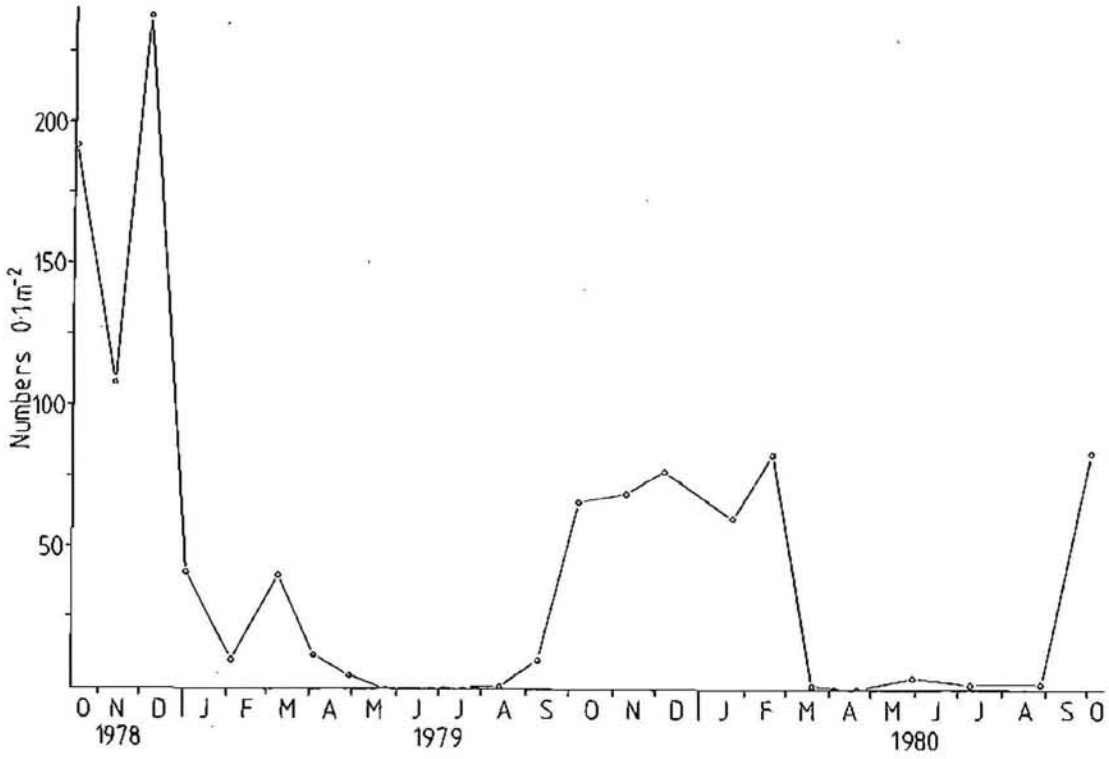

Fig. 8.5 Seasonal changes in density of early juveniles (<.450 mm h.l.) in the population.

Feb. - Mar. and varied somewhat between years. The occurrence of breeding was not strictly related to temperature; breeding began as water temperatures increased from the winter minimum and all but ceased in Feb. - Mar. while temperatures were far higher than the winter minimum (Fig. 3.4). During Apr. and July 1979, and in Mar., May - July 1980 appreciable proportions of the adult females carried broods (Fig. 8.6) but few juveniles hatched from these broods and entered the population (Fig. 8.5).

Broods consisting of early embryos (stages 1 - 2) were present at most times, whereas broods of later embryos (stages 3 - 4) and hatchlings (stage 5) were more seasonal in occurrence. Indeed, stage 4 - 5 embryos were present only during the summer period Oct. - Mar. noted above as the time of greatest reproductive activity and recruitment. The absence of embryos at later stages of development during winter months suggests that broods produced between Apr. and Aug. failed to complete development.

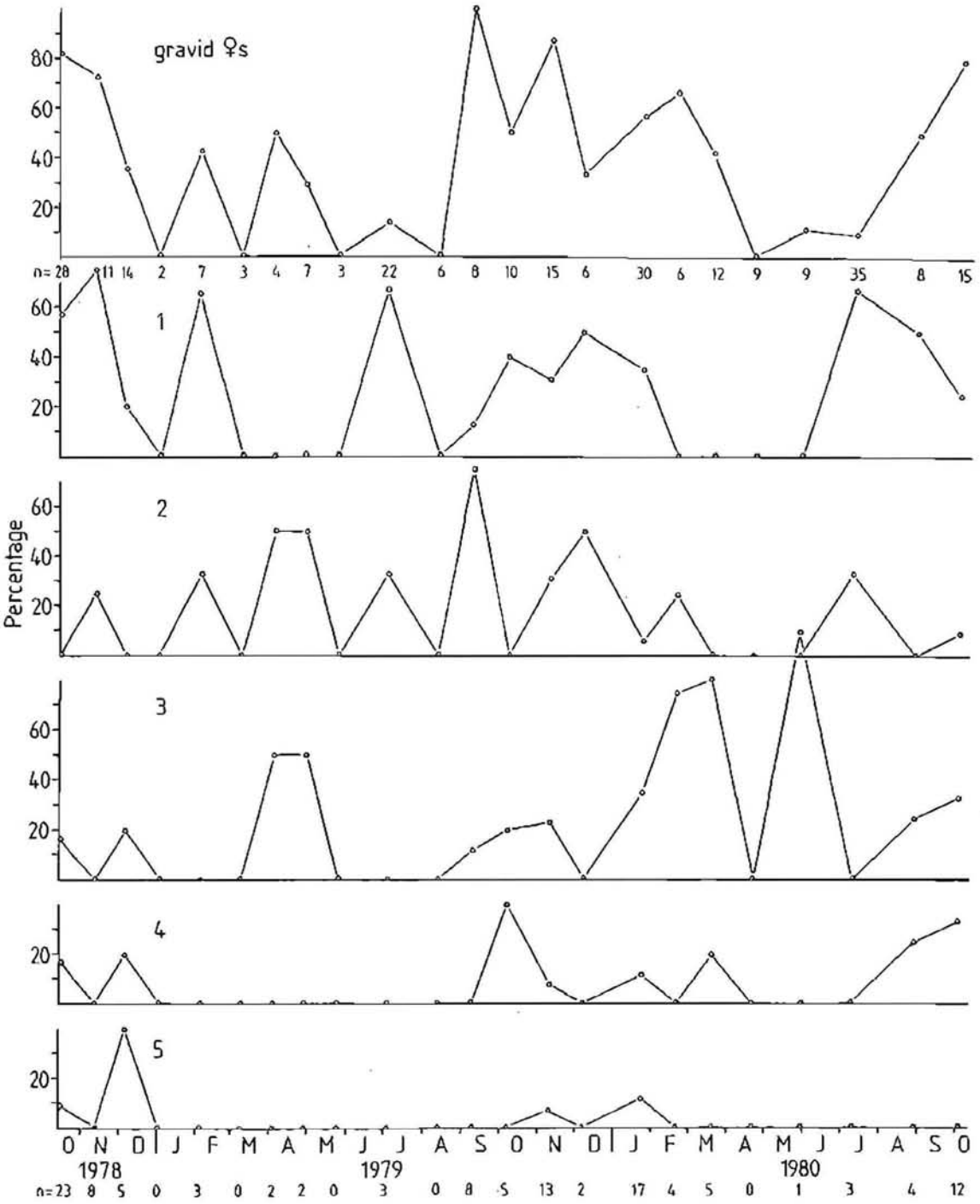

Fig. 8.6 Seasonal changes in the percentage of reproductive females (>1.000 mm h.l.) with broods and the percentage of broods at each stage of development.

EMBRYONIC DEVELOPMENT

Field data (Fig. 8.6) suggest that *Paraphoxus* embryos developed from stage 1 to 5 in about 95 - 109 days or about 100 days when corrected to 15°C. This estimate is unduly long and must be disregarded because six gravid females observed in the lab. (Appendix 5.1) provided a maximum embryonic development time of about 24 days at 15°C (Table 8.4). The median of 21 days thus seems a reasonable estimate of embryonic development time at 15°C for *Paraphoxus*.

Table 8.4 Duration of embryonic development for *Paraphoxus* at 15°C (see Appendix 5.1).

Development stage	Observed duration (days)
1	unknown, estimated 2 - 4
2	5 - 7
3	2 - 3
4	5
5	4 - 5
minimum duration	18
maximum duration	24

When egg (stage 1) size is considered then this estimate compares favourably with data available for other species (Steele & Steele, 1973, 1975c; Van Dolah *et al.*, 1975; Welton & Clarke, 1980).

Embryos increased in length by 23.5% during development from stage 1 to stage 4 (Table 8.5) but too few measurements were made to determine changes in volume reliably. An increase in embryo volume by about 30% between stages 1 and 4 is likely however.

During the 1978 - 79 summer, mean egg lengths decreased from 0.507 mm in

Table 8.5 Changes in mean length of embryos during development for *Paraphoxus*.

	Development stage 1	2	3	4
$\bar{x}$ length (mm)	.508	.491	.578	.664
SD	.044	.062	.071	.095
n	147	63	96	56
	t = 1.974	t = 8.165	t = 5.883	
	p <.05	p <<.001	p <<.001	
		t = 11.815		
		p <<.001		

Oct. to 0.458 mm by Feb. although the change between successive months was significant between Oct. and Nov. (Table 8.6). In the following summer mean egg lengths declined from Sept. to Nov. and then increased in Dec. and Jan. Thus smaller eggs may be produced as the population density increases during summer months and as the population becomes more density-dependent, perhaps as a consequence of food availability. Certainly during the first summer population densities were higher than in the second and the fewer storms could mean that food in the form of detritus and its consumers was less abundant. This interpretation is supported by the large and significant increase in egg length observed in Jan. 1980 when ten storm (waves >1.25 m high) days followed the previous sampling. An analysis of mean egg lengths for months grouped into seasons according to sea temperatures (Appendix 5.2) revealed little, and there was no relationship between mean egg length and mean monthly sea temperatures.

BROOD SIZE

Female *Paraphoxus* brooded 1 - 40 embryos and the mean brood number was 15.577 (SD = 7.149, n = 130). However, the mean number of eggs produced per

Table 8.6 Monthly mean egg (stage 1 embryo) lengths for *Paraphoxus* (months for which no data were collected have been omitted).

	Length (mm)			Significance	
	$\bar{x}$	SD	n	t	p
Oct. 78	.507	.031	39		
				3.428	<.01
Nov.	.474	.035	18		
				.375	n.s.
Dec.	.467	.029	3		
				.394	n.s.
Feb. 79	.458	.038	6		
				.138	n.s.
July	.479	.019	6		
				.302	n.s.
Sept.	.525	.025	3		
				.405	n.s.
Oct.	.515	.049	6		
				.881	n.s.
Nov.	.496	.028	12		
				1.050	n.s.
Dec.	.508	.014	3		
				3.354	<.01
Jan. 80	.543	.028	18		
				.420	n.s.
July	.533	.056	6		
				1.484	n.s.
Aug.	.492	.038	6		
				2.244	<.05
Oct.	.542	.048	9		

female is best detemined by considering stage two broods only to avoid errors arising from unfinished broods and from brood mortality. Thus the mean number of eggs produced per brood was 19.286. Brood size (stage 1 - 2 broods only) increased with female size according to the equation $Y = -3.610 + 18.102X$ ($r = 0.651$, $p < .01$) and consequently, monthly mean brood sizes tended to vary with the mean size of gravid females (Fig. 8.7). Apparent exceptions to this in July and Dec. 1979, when brood sizes increased and decreased respectively relative to female size, were probably a consequence of small sample sizes.

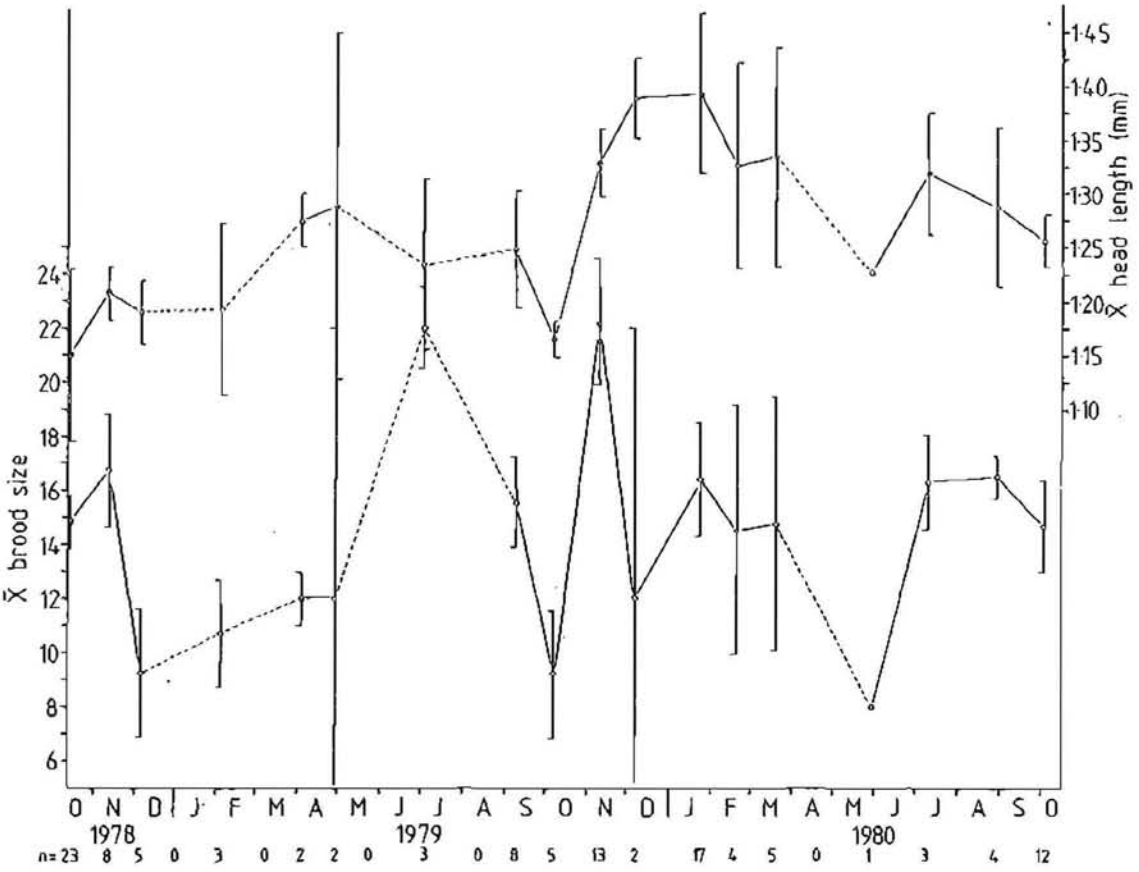

Fig. 8.7 Seasonal changes in the mean (± 1SE) brood size (stage 1 - 5 embryos) and mean (± 1SE) size of gravid females.

Both mean brood size and the size of gravid females then tend to be smaller during autumn, increase in midwinter and decline briefly in spring before increasing to summer maxima and then decreasing again in autumn. The pattern is however, irregular and complicated by year to year differences. In the first summer for example, the mean size of gravid females was 1.21 mm h.l. (Nov.) compared with 1.385 mm h.l. (Dec.) in the second summer. This difference and the associated increase in brood size possibly resulted from the warmer spring temperatures and the lower population density in 1979 - 80.

BROOD MORTALITY

There was a 34.5% mortality of *Paraphoxus* embryos during development from stage 2 to stage 4 (Table 8.7). The loss of one third of embryos before

Table 8.7 Brood size at each stage of embryonic development for *Paraphoxus*.

	Development stage				
	1	2	3	4	5
$\bar{x}$	16.260	19.286	16.333	12.632	7.714
SD	5.631	7.065	8.495	5.956	3.729
n	50	21	33	19	7
		$t = 3.230$			
		$p < .01$			

hatching seems high, but not unduly so when the large brood size of this species is considered. Further, females appear long-lived and probably produce two or more broods on average thus adequately compensating for the loss of embryos.

SEX RATIO

The *Paraphoxus* population sex ratio ($^{\sigma}/_{\varphi}$) was 0.398 (n = 464), or about 2.5 females per male. Figure 8.8A shows that females were sexable at a smaller size and attained a larger size than males. Also females were more abundant than males at all sizes. Largest juveniles were 1.1 mm h.l. and beyond this size males underwent the secondary sexual development of enlarged eyes and elongated second antennae. Recognition of males obviously was more reliable in the presence of these characters and at this size males constituted more than 40% of the population (Fig. 8.8B) bringing the sex ratio closer to parity. This indicates that the observed overall sex ratio was inaccurate because I could not sex small males reliably and because mortality of larger males was higher. The true population sex ratio probably is close to parity as indicated by the male probability curve (Fig. 8.8B).

Seasonal fluctuations in the population sex ratio (Fig. 8.9) resemble in pattern and magnitude the seasonal density of recruits in the population (Fig. 8.5). Peaks in the sex ratio plot, or increases in the proportion of males, preceeded each spring - summer recruitment period and male frequency

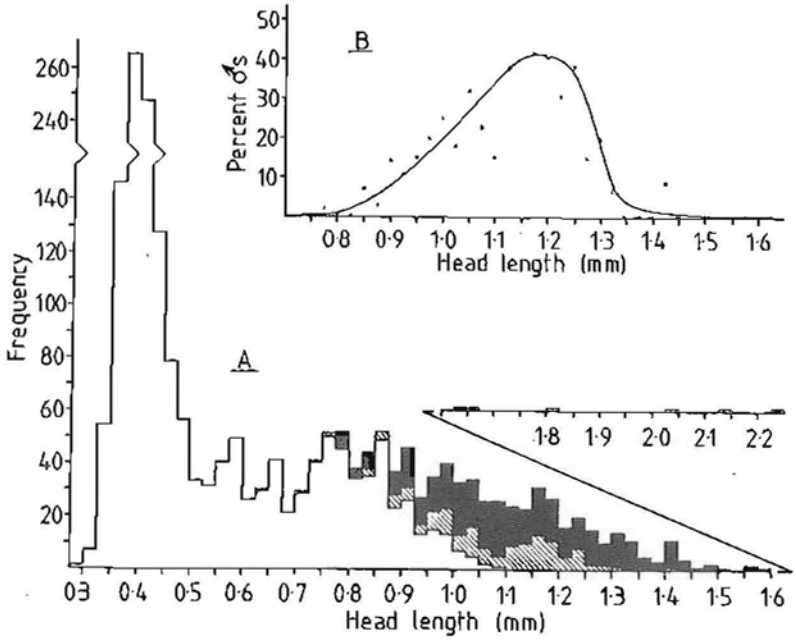

Fig. 8.8 *Paraphoxus* population size-frequency composition Oct. 1978 - Oct. 1980 (unshaded, juveniles; hatched, males; black, females) (A) and percentage frequency of males in each size class including unsexable juveniles (B).

decreased sharply before or with the decline in recruitment. Thus a significant correlation ($r = 0.646$, $p < .01$) was established between sex ratio and the density of new recruits about two months later ($Y = 3.869 + 62.785X$). Similarly, there was a significant ($r = 0.487$, $p < .05$) correlation between sex ratio and the frequency of adult females carrying broods about two months later ($Y = 10.345 + 71.247X$).

These relationships indicate that male puberty or maturity is carefully timed to preceed breeding periods so that mature males are available for mating as required. Further, the quantitative nature of both relationships imply that male availability limits the proportion of females which become gravid and ultimately determines the numbers of recruits produced and thus, the potential rate of population growth.

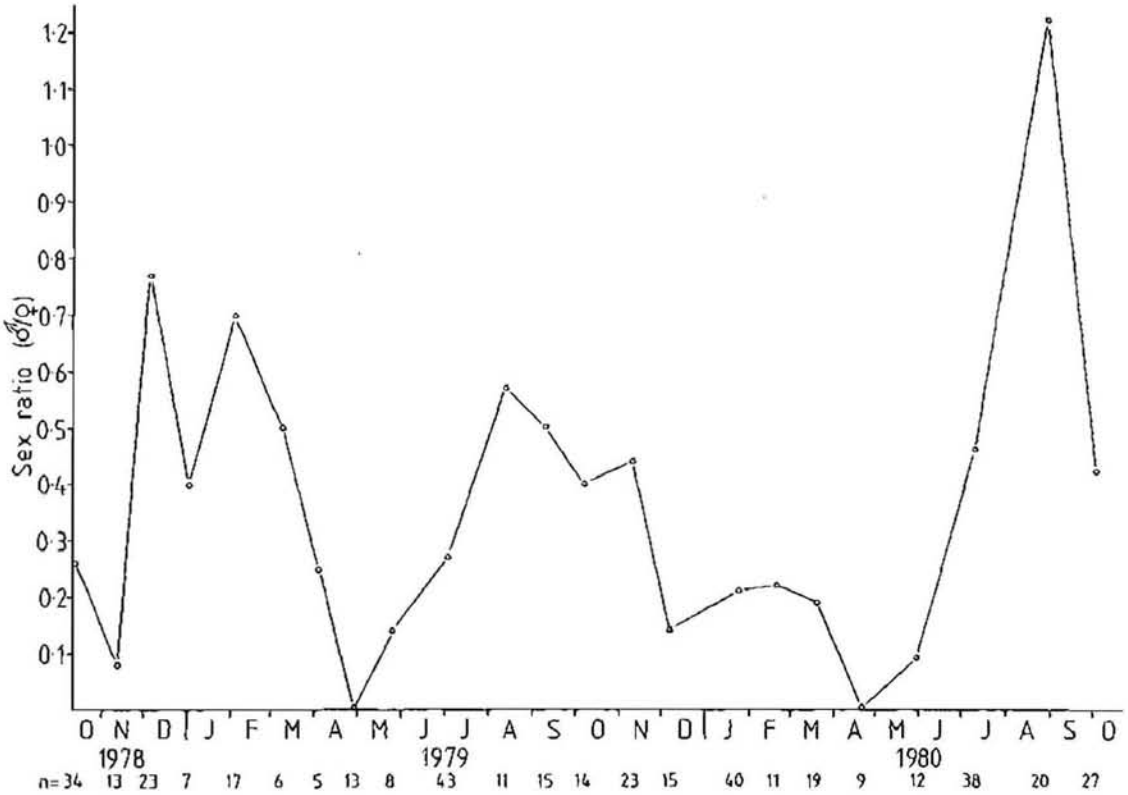

Fig. 8.9 Seasonal changes in sex ratio (♂/♀) of the total population.

CHAPTER 9

POPULATION BIOLOGY OF THE AMPHIPODA: THE KAIKOURA SPECIES IN PERSPECTIVE

POPULATION DYNAMICS

The life-histories of these four amphipods are characterised by faster-growing, shorter-lived summer cohorts and slower-growing, longer-lived winter cohorts. This pattern is typical of the northern hemisphere marine Gammaridea studied to date: *Ampelisca abdita, A. vadorum* (Mills, 1967), *A. brevicornis* off Marseilles (Kaim-Malka, 1969), *Bathyporeia pelagica, B. pilosa* (Fish & Preece, 1970), *Corophium arenarium, C. voluntator* (Fish & Mills, 1979), *C. bonnellii* (Moore, 1981), *C. insidiosum* (Sheader, 1978), *C. sextonae* (Hughes, 1978), and *Lembos websteri* (Moore, 1981). Further detailed studies will probably show this pattern to be even more widespread among species from areas with marked seasonal temperature changes with the obvious exception of annual univoltine species such as *Ampelisca brevicornis* in the Helgoland Bight and at the Isle of Man (Klein *et al*, 1975; Hastings, 1981), and *Talitrus saltator* (Williams, 1978). Unfortunately, most studies from areas other than the North Atlantic to date do not provide information on seasonal growth rates and cohort longevities.

The Kaikoura species populations consisted of between four and ten cohorts at any one time and they produced five to 12 cohorts annually. *Hippomedon* stands out among the others however, because its population consisted of only four and occasionally five cohorts and produced five cohorts per year. Although the *Paraphoxus* population consisted of five to nine cohorts, seven or eight new cohorts were recruited annually. Populations of *Corophium bonnellii* and *Lembos websteri* on British shores consisted of 3 - 6 and 5 - 6 cohorts respectively, but seven and nine cohorts respectively were added each year (Moore, 1981). Compared with these species then, the *Hippomedon* population consisted of few cohorts and their replacement rate was slow.

Despite this the seasonal and year to year population density variations of *Hippomedon* were less than for these other amphipods. It declined to 25% of the summer maximum during winter whereas winter densities of the other

species were less than 10% of their summer maxima and numerically lower than for *Hippomedon*.

OCCURRENCE OF BREEDING

Breeding and recruitment of all four species began in spring and its commencement seems closely tied to sea temperatures. Photoperiod (Segerstrale, 1970, 1971), temperature (Moore, 1978) or both (De March, 1977) influence the onset of breeding in amphipods generally. Photoperiod initiates gonad maturation in *Gammarus setosus* (Steele *et al*, 1977) but temperature seems to provide the ultimate stimulus to breed (Segerstrale, 1970, 1971; De March, 1977; Moore, 1981) so that a population may breed earlier or later with the timing of warmer sea temperatures. In the Kaikoura amphipods for example, water temperatures exceeded 11.5°C about one month earlier in 1979-80 than in the previous spring resulting in a larger, earlier peak recruitment by *Metaphoxus*. *Paraphoxus* recruitment began at about the same time in both springs however, and, although it was markedly lower in 1979 - 80, the continuation of warm (c.a. 16°C) sea temperatures into mid-Feb. resulted in moderate but constant recruitment throughout this period.

In addition to water temperature, food availability is an important influence on the level of breeding by the Kaikoura amphipods. Summer storms seemed to promote breeding activity indirectly by replenishing food sources through increasing the availability of finely fragmented macro-algae and detritus. Moore (1981) also considered that more frequent stormy conditions in one year provided abundant food particles for *Lembos websteri* and prompted an unusually early commencement of breeding. The second summer, 1979 - 80, was characterised by more frequent storms and three species showed various responses: Breeding of *Patuki* was prolonged and larger eggs were produced; the total *Metaphoxus* population was larger, females attained a greater size and produced more eggs; recruitment continued longer in *Paraphoxus* and larger eggs were produced in late summer.

Storms apparently also provide a means of partially synchronizing breeding by different cohorts of *Hippomedon* and *Patuki*. Brood production was stimulated directly in *Hippomedon* females with mature ova, and indirectly in other females by increasing available food supplies. Synchronous breeding of *Patuki* cohorts occurred at new moons but the intensity of breeding activity at each new moon decreased with increasing time since the last storm.

Synchronous breeding with lunar and semi-lunar periodicities are common among shallow sublittoral and intertidal amphipods (Mills, 1967; Hastings, 1981; Moore, 1981) and the adaptive significance of such periodicities to sublittoral species was discussed by Moore (1981).

Application of growth factors to predict the number of instars for species of amphipods must be done with caution and such estimates provide a crude guide at best. Moore (1981) applied a factor of 1.25 to *Lembos websteri* and *Corophium bonnellii* following Thurston's (1968) (who applied this factor to *Bovallia gigantea*) derivation of a mean growth factor (range 1.20 to 1.33) from Sexton's (1924) illustrations of instars 1 - 8 (maturity at instar 8, maximum instars 26 (Sexton, 1924)) of *Gammarus chevreuxi*. Wildish (1979) reported a growth factor of 1.12 for *Orchestia* spp. However, it is generally known that the premoult - postmoult size relationship differs between species and that it usually changes with size and age in most species (Kurata, 1962). Growth factors for *Corophium insidiosum* and *Jassa falcata* calculated from Nair & Anger (1979a,b) show a decrease with the onset of female maturity. Hence two growth factors should be used in estimating the sizes and number of instars for amphipod species, a pre-maturity factor of 1.20 and a post-maturity factor of 1.06, values in accordance with those for *Corophium insidiosum* and *Jassa falcata* and which produce reasonable results (Table 9.1).

Thus female *Metaphoxus* apparently mature in their fourth instar, *Hippomedon* in their fifth, *Patuki* in their sixth and the larger *Paraphoxus* females in their seventh instar and females of each species may produce up to seven, seven, 11 and 13 broods per life-time respectively. These estimates and those of maximum numbers of instars per female compare favourably with similar estimates for other amphipods (Table 9.2), especially those estimates determined by rearing individuals. Sheader (1979) reported that both sexes of *Corophium insidiosum* matured in their fourth instars and grew through a total of nine instars. In their study of the same species, Nair & Anger (1979a) reported marked parent age (status of brood) and temperature effects on size and instar at the attainment of sexual maturity and on individual longevity. Within either brood status category, warmer temperatures prompted maturity up to 1 instar earlier and at a smaller size than at cooler temperatures. Maturity occurred in instars 4 - 6 for females and one instar earlier in males, and females lived to at least instar 15 in some treatments (Nair & Anger, 1979a). *Jassa falcata* matured in instar 5 - 6 and may pass

Table 9.1 Sizes (head lengths, mm) of instars for each amphipod estimated by applying a pre-maturity growth factor of 1.20 and a post-maturity growth factor of 1.06 to the mean size of hatchlings (development stage 5) (m, first mature instar producing offspring; ( ), few females attain this size).

	Hippomedon	*Patuki*	*Metaphoxus*	*Paraphoxus*
$\bar{x}$ hatchling size	.206	.362	.340	.367
size at ♀ maturity	.350	.800	.551	1.000
maximum ♀ size	.525	1.400	.825	2.175
instar				
1 (hatchling)	.206	.362	.340	.367
2	.247	.434	.408	.440
3	.297	.521	.490	.529
4	.356 m	.625	.588 m	.634
5	.377	.751	.623	.761
6	.400	.796 m	.660	.913
7	.424	.843	.700	1.096 m
8	.449	.894	.742	1.162
9	.476	.948	.786	1.231
10	.505	1.005	.833	1.305
11	.535	1.065		1.384
12		1.129		1.467
13		1.196		1.554
14		1.268		1.648
15		(1.344)		(1.747)
16		(1.425)		(1.851)
17				(1.963)
18				(2.080)
19				(2.205)
total instars	11	16	9	19

Table 9.2 Maturity, maximum size and maximum numbers of instars and broods of female marine gammaridean amphipods (*, maximum number of broods per female inferred assuming one brood per instar after maturity; [A], Antarctic species; F, field data).

Species	maximum total length (mm)	maximum no. instars	instar at maturity	maximum no. broods/female	method	source
Corophium bonnellii	5.5	6	3	3*	Brook's Law	Moore, 1981
C. insidiosum	5.6	13	4-6	7	lab. culture	Nair & Anger, 1979a
C. insidiosum	4.4	9	4	6*	lab. culture	Sheader, 1978
Gammarus duebeni	18.4	27	14	6F	lab. culture	Kinne, 1959
Gammarus chevreuxi	9.0	34	8	26	lab. culture	Sexton, 1928
Jassa falcata	7.8-8.9	7-9	4-5	4-5*	lab. culture	Nair & Anger, 1979b
Lembos websteri	6.0	9	6	4*	Brook's Law	Moore, 1981
Microdeutopus gryllotalpa	8.0	21	10	11	lab. culture	Myers, 1971
Hippomedon whero	6.7	11	5	7*	Brook's Law	present report
Patuki roperi	10.0	16	6	11*	Brook's Law	present report
Metaphoxus littoralis	4.6	9	4	7*	Brook's Law	present report
Paraphoxus australis	14.0	19	7	13*	Brook's Law	present report
[A]*Bovallia gigantea*	50.0	13	12	1	Brook's Law	Thurston, 1968
[A]*Paramoera walkeri*	22.8	14	3	12*	polymodal analysis	Sagar, 1980

through as many as ten instars (Nair & Anger, 1979b). *Gammarus chevreuxi* matures in its ninth instar subsequently producing up to 26 broods in successive instars (Sexton, 1928) and *Microdeutopus gryllotalpa* in its tenth instar with some females surviving through 21 instars (Myers, 1971). *Lembos websteri* and *Corophium bonnellii* were considered to mature in their sixth and fourth instars and pass through nine and seven instars respectively (Moore, 1981) but these were derived by application of a growth factor of 1.25.

EMBRYONIC DEVELOPMENT

It is now well established that development times of gammaridean embryos decrease in a curvilinear manner with increasing temperature (Vlasblom, 1969; Steele & Steele, 1973, 1975c; Van Dolah *et al.*, 1975; Welton & Clarke, 1980; Sutcliffe & Carrick, 1981; Omori *et al.*, 1982) but the relationship has been investigated thoroughly in few species of only four genera, two of which are exclusively freshwater in occurrence. Similarly, the less well understood relationship between amphipod egg sizes and their durations of development was investigated for *Gammarus* spp. only and very few additional data have become available since Steele & Steele's (1975c) study. Three major problems arise in comparing published data: First, development times determined at various temperatures must be corrected to a standard, preferably 10°C, a problem compounded by the next. Second, none of the published equations (Bottrell, 1975; Van Dolah *et al.*, 1975; Welton & Clarke, 1980; Sutcliffe & Carrick, 1981) describing the development time - temperature relationship considers the effect of egg size, a consequence of single species studies but a significant failing in view of Steele & Steele's (1975c) findings. Third, different workers measured fresh or variously preserved egg sizes in different ways (e.g. maximum length, mean of length + breadth). In attempting to extend Steele & Steele's (1975c) relationship I corrected development times to 10°C using Q_{10} values determined by Welton & Clarke (1980) for *Gammarus pulex*: Q_{10} = 3.64 for 5 - 10°C, 2.33 for 10 - 15°C and 1.56 for 15 - 20°C. Rates determined at less than 5°C were corrected to 10°C using the higher Q_{10} value of 3.64.

Data for *Patuki*, *Metaphoxus* and *Paraphoxus* are grouped closely with those for *Gammarus* spp. (Fig. 9.1). Other points derived from the literature and corrected as above produce a broad scatter masking the discreteness of Steele & Steele's (1973) original linear relationship, but nonetheless indicating that

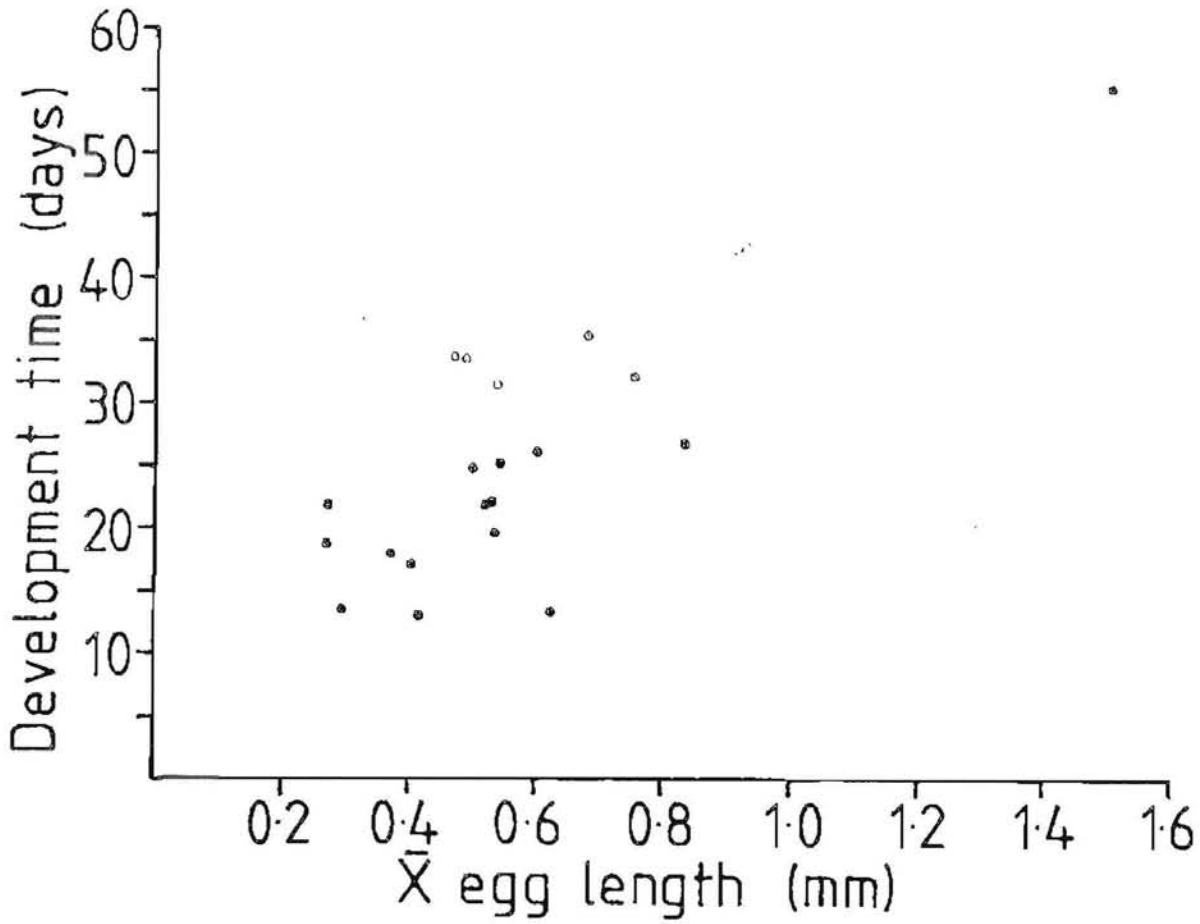

Fig. 9.1 Relationship between amphipod egg (stage 1) size and duration of development. Data from Thurston (1968), Sheader & Chia (1970), Bregazzi (1973), Steele & Steele (1973), Fish (1975), Sheader (1978), Nair & Anger (1979a) corrected to 10°C using Q_{10} values from Welton & Clarke (1980).

the duration of development does increase linearly with egg size. In a study of the effect of egg size on development time for one species of mysid, Whittman (1981) found a similar positive linear relationship with equally high variation, and concluded that the effect of egg size on development rate was small compared to the temperature effect.

EGG SIZE AND BROOD SIZE

Egg (stage 1) sizes of the Kaikoura amphipods ranged between 0.375 and 0.532 mm length with *Patuki*, the largest species, producing the largest eggs

and the smallest species, *Metaphoxus*, producing smallest eggs. In a comprehensive analysis of amphipod reproductive patterns, Nelson (1980) found a positive correlation between minimum reproductive female size and egg size for 39 species. The Kaikoura species fall well within the array of points forming this relationship (Fig. 9.2). Moore (1981) discussed possible reasons for differences in egg sizes among species of *Corophium* and considered that the substantially larger (twice) eggs of *C. bonnellii* were a consequence of its parthenogenetic reproduction. Unfortunately data for this species cannot be included in Fig. 9.2 because Moore (1978, 1981) measured head length only and provided no indication of its relationship to total length.

Similarly the positive relationship between brood size (or egg number) and female size in amphipods has been discussed at length (Steele & Steele,

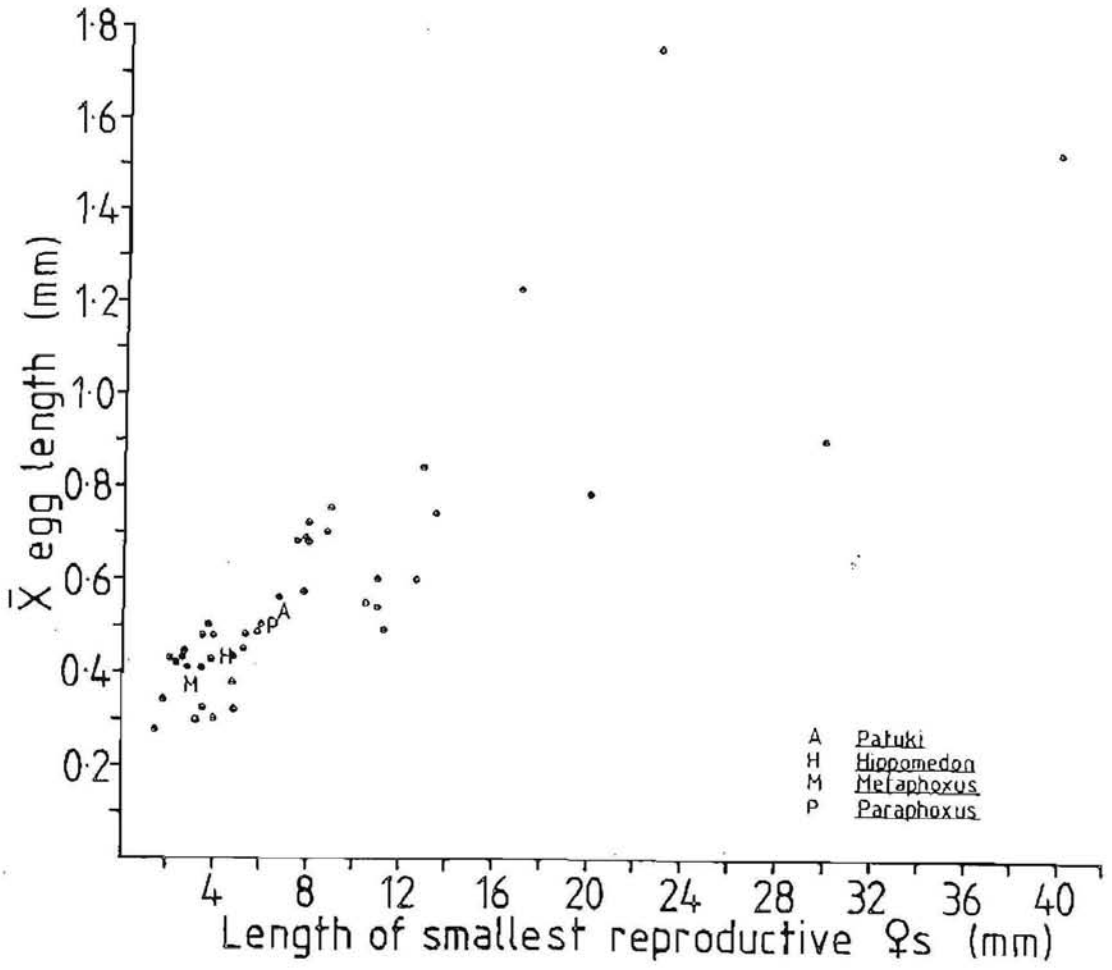

Fig. 9.2 Relationship between minimum size of reproductive females and mean egg (stage 1) length. Data mostly from Nelson (1980).

1975b; Nelson, 1980; Van Dolah & Bird, 1980; Moore 1981) but the nature of this relationship remains questionable. Several authors considered it to be simply linear, whilst others claimed that brood size was expotentially related to female length and hence linearly to female volume. In reviewing the subject Moore (1981) felt that ovary shape and dimensions could be important, especially in small species, and that in larger species (e.g. *Lembos websteri* (Moore, 1978)) the apparent curvilinear broodsize - female size relationship resulted from variation in size or instar at first breeding and a minimum - sized first brood. Thus such relationships conceivably consist of two linear components: An initial component where brood size and female size are independent, and a second component where the two increased linearly together (Moore, 1981). A third component where brood size decreased with increasing female size as a consequence of senility was also suggested by Moore (1981). Although I performed only linear regressions on brood size - female size data for the Kaikoura species, the high levels of significance ($p < .001$ for *Hippomedon* and *Patuki*, $p < .01$ for *Metaphoxus* and *Paraphoxus*) indicate that the relationship was indeed linear in each of these species. Moreover, examination of the data indicated that the relationships were neither curvilinear nor composed of two or more linear components.

Seasonal differences in egg (stage 1) sizes observed in two Kaikoura species revealed an inverse relationship between egg size (length) and water temperature during at least part of the year. Variation in egg size with season has received almost no attention despite the well established correlation between egg size and female size at maturity (Nelson, 1980) and the tendency for females of many amphipods to mature at larger sizes and in later instars when exposed to cooler temperatures (Nair & Anger, 1979a; Moore, 1981). Steele & Steele (1969, 1970b) found that *Gammarus duebeni* and *G. obtusatus* eggs were significantly larger during winter than in summer and presumably this is true for the other species of *Gammarus* included in their (Steele & Steele, 1975a) types 2 and 3 reproductive patterns. In a series of rearing experiments Nair & Anger (1979a) confirmed that the sizes of eggs produced by individual female *Corophium insidiosum* did change, in this case increasing with age and presumably size of the females. The longer development time concomitant with larger winter eggs means that embryos will hatch either in or closer to more favourable spring temperature and food conditions. Further, these hatchlings will possess a greater ecological fitness because of their larger size (Thorson, 1950; Smith & Fretwell, 1974),

and thus larger proportions of such cohorts would survive to breed under optimal spring/summer conditions. These observations suggest then, that seasonal alteration of egg size may be an important mechanism delaying hatching of winter embryos until more favourable conditions prevail and to enhance recruitment by producing larger, fitter hatchlings. Other species in which females mature at larger sizes in winter than in summer and produce several cohorts annually include *Corophium insidiosum* (Sheader, 1978), *C. arenarium* and *C. volutator* (Fish & Mills, 1979), *C. bonnelli* and *Lembos websteri* (Moore, 1981), *Neohaustorius schmitzi* (Dexter, 1971), *Bathyporeia pelagica* and *B. pilosa* (Fish & Preece, 1970) and *Gammarus chevreuxi* (Sexton, 1928). This may be some indication of the frequency of seasonal egg size variation among the Amphipoda generally.

It should be noted however, that this inverse egg-size - temperature relationship did not hold at all times for *Hippomedon* and *Patuki*. During the 1979 - 80 summer their eggs were larger than expected, possibly a consequence of unusually abundant food following a series of storms.

Amphipod embryos typically increase in volume by over 200% during development (Sheader & Chia, 1970; Thurston, 1968; Bregazzi, 1973; Sheader, 1978; Williams, 1978; Fish & Mills, 1979; Moore, 1981) due to a steady osmotic uptake of water (Davis, 1968; Bregazzi, 1973). Changes in embryo volume observed for the Kaikoura species were rather low in comparison (*Hippomedon*, 150%; *Patuki*, 131%; *Metaphoxus*, 179%) and more similar to the c.a. 144% increases observed for embryos of *Bathyporeia pelagica* and *B. pilosa* (Fish, 1975). Increases of embryo lengths for three of the Kaikoura species (120 - 132%) are much the same as for other amphipods (130 - 170%) (Thurston, 1968; Sheader & Chia, 1970; Bregazzi, 1973; Fish, 1975; Williams, 1978; Moore, 1981). *Hippomedon* proved rather unusual in exhibiting a 171% increase in embryo length during development, considerably higher than for the other Kaikoura species. Steele & Steele (1969, 1970a,b,c, 1972) measured embryo size as length + width/2 for *Gammarus* species and recorded increases of 134 - 159% with development (stages A - D, Steele & Steele, 1969). A similar increase occurred in *Gammarellus angulosus* (Steele & Steele, 1972) but examination of preserved *Amphiporeia lawrenciana* (Downer & Steele, 1979) indicated a size increase of only 110%.

BROOD MORTALITY

Brood mortality is widespread among marine peracarids and in the Amphipoda between 20 and 30% of embryos usually do not complete development (Moore, 1981, table XVII). In two antarctic amphipods brood mortalities were considerably lower; less than 1% in *Cheirimedon femoratus* and 10% in *Hippomedon kergueleni* (taken from Bregazzi's (1972) figs. 11 & 25). The two phoxocephalids from Kaikoura exhibited brood mortalities of 30.4 and 34.5%, well within the range for other marine amphipods, but the 30.4% mortality of *Metaphoxus* broods seems remarkably high relative to its mean brood size (2.7) when compared with that of *Paraphoxus* (19.3). *Hippomedon* broods suffer 14.2% mortality, low for a temperate amphipod and more similar to that of its antarctic congener *H. kergueleni*. Perhaps species of the Lysianassidae, which includes *Hippomedon* and *Cheirimedon*, generally have lower brood mortalities than species of other families studied to date, the Corophiidae, the Gammaridae, the Phoxocephalidae, the Haustoriidae and the Talitridae, although terrestrial species of this family prove exceptions (Wildish, 1979). The deep, overlapping coxae of many lysianassids form a variously enclosed ventral chamber including the marsupium and this may reduce accidental egg losses. Enclosing is almost complete in at least one genus and there has been a progressive loss of oostegites with adult females of some species possessing three or two pairs or completely lacking oostegites (Lowry *et al.*, in prep.).

Zero brood mortality occurs in *Patuki* (family Oedicerotidae), the remaining Kaikoura species. This is surprising since *Patuki* is a highly mobile species dwelling at the water - sand interface and producing large broods (1 - 24 eggs, $\bar{x}$ = 6.7). Again however, its coxae are deep, curved medially and form an overlapping array along each side of the marsupium. Oostegites are long and, although narrow, they are armed with long, stout setae marginally and distally. Moreover, *Patuki* embryos increase in volume by only 130.6% (121.5% length increase) during development, thus minimizing distention of the marsupium and consequently, the probability of accidental embryo losses. In other amphipods exhibiting zero brood mortality (*Cheirimedon femoratus*, *Orchestia* spp.), there was a normal (>200%) increase in embryo volume during development (Bregazzi, 1972, 1973; Wildish, 1979).

The effect of female size on brood mortality has been examined for two species and size - specific brood mortalities for *Cheirimedon femoratus* and

Hippomedon kergueleni were extrapolated from Bregazzi (1972). Brood mortality was essentially zero in all sizes of *Cheirimedon femoratus*. In *Talitrus saltator* and *Hippomedon kergueleni* there was a slight increase in brood mortality in larger females and a decrease in largest females (Bregazzi, 1972; Williams, 1978). Brood mortality increased with female size in *Corophium bonnellii* (Moore, 1981). Size related brood mortality was not apparent in *Hippomedon*, *Patuki* or *Metaphoxus* from Kaikoura, but sample sizes were rather small. These findings suggest that the effect of female size on brood mortality may differ between species, genera or families of amphipods.

SEX RATIO

Sex ratios of three of the Kaikoura amphipods were quite unusual in their significant deviations from parity. Most remarkable was the overall sex ratios ($^{\sigma}/_{\varphi}$) of 2.09 for *Hippomedon*. In only one of the 18 seasonal samples was the sex ratio in favour of females and on three occasions there were more than three males per female. This predominance of males was not due to their recognition and maturity at a smaller size alone (Fig. 5.10). Indeed, even at the size of male puberty the population is biased in favour of males and subsequently the bias is exaggerated by different growth rates and by selective mortality.

This initial disparity may be inherited either genetically or epigenetically so that male hatchlings outnumber female hatchlings. Rather complex and different modes of sex determination occur in the few amphipod species so far investigated (Bulnheim, 1978). Sex ratios of offspring may deviate from normal (1:1) and become amphogenic (progeny of both sexes in different proportions) or monogenic (progeny all same sex), either thelygenic (all female) or arrhenogenic (all male), resulting from an interplay of "a poly-factorial system of sex genes and modifying environmental factors" (Bulnheim, 1978). Day length alone, operating during the early post-hatchling juvenile period determined the sexes of *Gammarus duebeni duebeni* and *G. zaddachi* (but not *G. locusta*) resulting in thelygenic broods with short (8 h) days and arrhenogenic broods with long (16 h) days. Ovarian infection by microsporidian parasites transmitted via eggs exerted a complete feminizing effect, cancelling the effect of day length but inhibited by low (<4°C) temperatures and suppressed by higher than normal salinities. Two species of microsporidians have been identified and infection by either one or both induces the feminizing

effect. Most populations of *G. d. duebeni* examined were infected and in some, more than 50% of females were infected (Bulnheim, 1978). The sex ratios of infected populations thus could deviate far from unity in favour of females, and in uninfected populations seasonal sex ratio disparities could be induced by changes in day length.

The erratic seasonal sex ratio fluctuations of the *Hippomedon* population and of the other three species preclude the possibility of photosensitive sex determination. Microsporidian infection is feminizing in effect and so, on the basis of present knowledge, does not explain the predominance of male *Hippomedon*. The mechanism of the feminizing effect is unknown however, and it is not inconceivable that a microsporidian or similar protistan infection could exert a masculinizing effect in some amphipods. In the absence of any evidence for such infection, a masculinizing effect remains hypothetical and unlikely.

Apart from its sex ratio there is no evidence suggesting incomplete sampling of the *Hippomedon* population due to migrations. Investigation of its sediment depth distribution (Chapter 10) indicated that although females dwelt deeper in the sediment than males, their centre of distribution was shallower than 180 mm (maximum sampling depth) and the porportion of females missed was relatively small. The density of developing embryos was similar to the density of new recruits (<0.250 mm h.l.) found in the following month (Table 9.3). In three instances only were there appreciable deficits between embryo and subsequent recruit densities: Nov. - Dec. 1978, Nov. - Dec. 1979, Dec. 1979 - Jan. 1980. At these times broods were probably produced, hatched and released between successive samples due to acceleration of embryonic development by the prevailing high (17°C) sea temperatures.

Selective predation and other female mortality, possibly a consequence of brooding, may be important in increasing the population sex disparity. Sexual dimorphism is minimal in *Hippomedon* (Fenwick, in press) except that females grew larger and were somewhat stouter than males. Possibly females were not as rapid burrowers as males and brooding could further slow their burrowing rates. Size and sex selection of amphipod prey are known: Nelson (1979) found selection of small amphipods by shrimps but not by fishes whereas Moore (1981) noted that fishes selected larger amphipods. In addition, shrimps selected more females than males of two sexually dimorphic species, but equal numbers of a less dimorphic species (Nelson, 1979). Thus *Hippomedon's*

Table 9.3 Seasonal fecundity and recruitment of *Hippomedon whero* (new recruits = <0.250 mm h.l.).

	$\bar{x}$ gravid ♀s $0.1m^{-2}$	$\bar{x}$ brood size	$\bar{x}$ embryos $0.1m^{-2}$	$\bar{x}$ new recruits $0.1m^{-2}$
Oct. 1978	60.0	3.70	222.0	162
Nov.	28.0	2.91	81.48	93
Dec.	52.0	4.23	219.96	212
Jan. 1979	26.67	4.20	112.01	99
Feb.	25.6	2.56	65.54	26
Mar.	32.0	3.17	101.44	50
Apr.	16.0	2.0	32.0	12
Apr.	16.0	1.67	26.72	24
May	18.0	2.56	46.08	0
July	13.0	1.62	21.06	3
Aug.	28.0	2.75	77.0	3
Sept.	19.0	3.58	68.02	39
Oct.	47.0	3.75	176.25	83
Nov.	22.67	4.06	92.04	90
Dec.	20.8	3.0	62.4	157
Jan. 1980	22.4	3.50	78.4	39
Feb.	10.67	3.25	34.68	101
Mar.	10.0	1.70	17.0	6

highly disparate sex ratio may result from a slight genetical predominance of males accentuated by selective predation of larger, faster-growing, and possibly less elusive females.

The population sex ratio of *Patuki* was essentially at parity as were those for *Metaphoxus* and *Paraphoxus* when their sexual size differences at puberty and the shorter longevity of males are taken into account.

Seasonal sex ratio fluctuations in *Hippomedon*, *Patuki* and *Paraphoxus* indicated that male puberty or maturity is carefully timed to preceed brood release and new brood production so that abundant males are available for mating just when required. Thus while breeding activities are simultaneous between sexes and synchronous with moulting for females, the male moult cycle, at least at maturity, preceeds that of females and has a synchrony of its own. Further, in *Paraphoxus* there is some indication that the availability of males limits the number of females that become gravid, and ultimately the number of new recruits produced.

CHAPTER 10

PARTITIONING OF A RIPPLED SAND HABITAT BY FIVE INFAUNAL CRUSTACEANS

INTRODUCTION

Sediment depth has always been accepted as an important factor in the distribution of benthic infauna, but surprisingly few attempts have been made to quantify infaunal changes with sediment depth. Horizontal spatial pattern of and space partitioning by macrofauna has recently received more attention (Angel & Angel, 1967; Johnson, 1967; Reys, 1971; Levinton, 1972; Gage & Geekie, 1973; Gage & Coghill, 1977; Eckman, 1979; Oliver *et al.* 1980). Two studies examined the sediment depth distribution: Oliver *et al.* (1980) examined the macrofauna (Crustacea, Mollusca, Vermes and one species of echinoid), while Croker & Hatfield (1980) studied space partitioning by three intertidal amphipods over several years. A few studies on meiofauna dealt with space partitioning (e.g. McLachlan *et al.*, 1977; Bell *et al.*, 1978), but only Harris's (1972) work considered individual species' depth distributions and their temporal changes. Following Eckman's (1979) study which suggested that small macrobenthic animals were distributed in response to locally varying hydrodynamic micro-habitats resulting from water movement over sediment ripples, Hogue & Miller (1981) showed that nematodes collectively, were distributed in response to small-scale environmental heterogeneity produced by current-induced sediment microtopography (ripples).

In South Bay, Kaikoura, New Zealand, the coarse, shelly sand bottom consisted of large (150 - 200 mm high), widely spaced (350 - 400 mm) ripples produced by wave action and provided an excellent opportunity to examine differences in infauna with ripple position. Further, the small number (five) of very abundant species in this habitat made comparisons of species vertical space utilization relatively simple.

METHODS

A description of the South Bay study area was given in a previous section (Chapter 3). During Sept. 1979 the median diameter of sand was 1.40 ø, well within the range observed during the entire study.

Sample points were located using the 2-digit random number method outlined in Chapter 3 except that where necessary the sample point was moved clockwise on the fixed radius to locate the nearest ripple crest or trough. Immediately on removal of the 187 mm long corer from the sediment it was inverted, placed in a close-fitting plastic bag and firmly tapped on the bottom 3-4 times to compact the sediment and thus reduce movement of the sampled animals. The cores were then kept inverted until sectioned at the lab. within 1.5 h. This procedure of consolidating the sediment and storing inverted seemed to prevent appreciable movement of the crustaceans because their distributions in the sectioned cores agreed with observations on their dwelling depths in situ and with the results of some preliminary lab. experiments. Four replicate cores were taken from ripple troughs and four from crests on each sampling date.

Compacted, drained cores were removed intact from corers and sectioned into the following layers: 0 - 20, 20 - 60, 60 - 100, 100 - 140, 140 - c.a. 170 mm. Animals were removed from each section by the combination of kerosene floatation and decanting through a 0.30 mm sieve several times as described earlier. Sorting, measuring and sexing of individuals was undertaken as previously outlined. Final data analysis considered the upper four layers to 140 mm depth only because examination of the data revealed that the deepest layer (140 - 170 mm) of some cores included individuals from shallower layers that had remained in sand adhering to the corers sides and were subsequently included in the deepest layer. For example, successive layers from one core yielded 14, 6, 2, 0, 3 *Metaphoxus*, a species known from lab. and field observations to inhabit the shallower sediment depths. Instead of attempting to correct suspect 140 - 170 mm layers, I decided upon the more rigorous approach of excluding this lower layer completely, especially since the centres of abundance of all species were well above 140 mm.

RESULTS

CYCLOLEBERIS ZEALANDICA

Within instars IV - VI there were no significant differences (t-tests, $p > .05$) in the mean densities of each sex with ripple position (Appendix 6.1). Instar VII was excluded from this analysis because of the scarcity of males (see Chapter 4). As a result, sexes were not distinguished in further analyses of the effect of ripple position on density. Further analysis (Table 10.1) showed that neither the density of each instar, nor the total population density (Table 10.2) differed significantly with ripple position.

Table 10.1 Differences in mean densities (nos 0.05 m^{-2}) of *Cycloleberis* instars with ripple position (data from Aug., Sept., Oct., Dec. 1979, Mar., Aug., Oct. 1980).

Instar	Density (nos 0.05 m^{-2})				Significance	
	Troughs		Crests			
	$\bar{x}$	SD	$\bar{x}$	SD	t	p
I	1.429	2.992	0.857	1.464	0.454	ns
II	1.143	1.464	0.857	1.464	0.366	ns
III	2.186	2.170	0.429	0.787	2.014	ns
IV	6.471	4.570	4.90	3.342	0.734	ns
V	11.286	13.793	5.186	4.576	1.111	ns
VI	15.0	7.572	9.857	8.513	1.194	ns
VII	7.814	5.542	8.529	8.667	0.184	ns

Table 10.2 Differences in *Cycloleberis* mean population density (nos 0.0125 m^{-2}) with ripple position.

	Troughs			Crests				
Sample	$\bar{x}$	SD	n	$\bar{x}$	SD	n	t	p
Aug.'79	5.75	3.304	4	1.75	0.957	4	2.326	ns
Sept.'79	4.50	2.887	4	5.0	4.320	4	0.193	ns
Oct.'79	11.25	4.646	4	5.5	3.109	4	2.057	ns
Dec.'79	26.333	10.504	3	20.75	2.630	4	0.900	ns
Mar.'80	8.00	1.414	4	6.75	4.646	4	0.721	ns
Aug.'80	8.75	5.56	4	5.25	3.096	4	1.099	ns
Oct.'80	14.25	4.425	4	9.667	6.028	4	1.226	ns

Instars IV - VII only were common in the two sets of sectioned cores and pooled replicates data were analysed by four-way factorial anova (Appendix 6.2). Samples contained too few individuals for analysis of sex-related differences but Fig. 10.1 indicates that both sexes have similar distributions. There were no significant interactions between instar, time, ripple position, and sediment depth, and depth was found to be the only gross effect with which instar frequency varied significantly (F_s = 5.510, $dfs_{n_1 n_2}$ = 3, 9, p <.05).

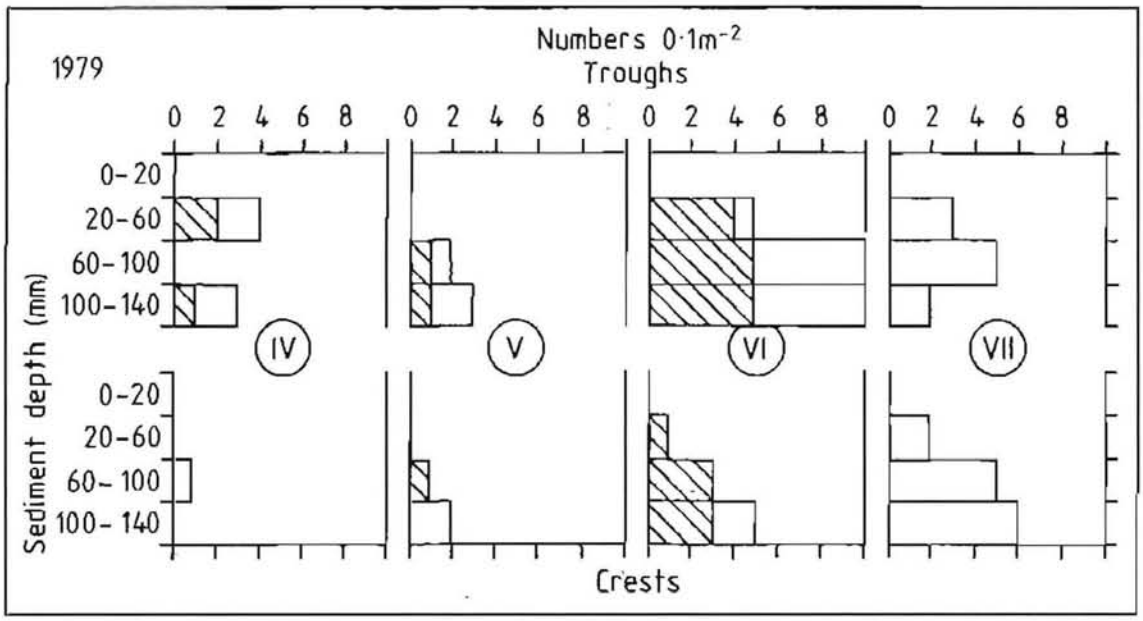

Fig. 10.1 The effect of ripple position on sediment-depth distributions of *Cycloleberis* instars IV - VII (data for Sept. and Oct. 1979 pooled) (shading, gravid females).

Since the anova detected no significant interactions between depth and time, and between depth and ripple position, the mean depth inhabited by each instar was calculated from the pooled data (Table 10.3). There were no significant differences (t-tests, p <.05) in mean depths inhabited by instars and the overall mean depth inhabited by *Cycloleberis* instars IV - VII was 88.22 mm. In the laboratory five and six individuals out of two sets of seven animals inhabited the 20 - 60 mm layer 2.5 hours after being placed in the experimental tubes of sand. The mean depth occupied by these experimental animals (46.43 mm, SD = 25.30, n = 14) was significantly (t = 5.437, p <.001) shallower than that inhabited by core-sampled ostracods. Experimental effects probably produced this difference. In particular, the rate of water flow

Table 10.3 Mean depths inhabited by instars IV - VII of *Cycloleberis*.

Depth (mm)	Instar IV	V	VI	VII	IV - VII
$\bar{x}$	75.00	100.00	90.59	85.22	88.22
SD	39.64	30.24	30.05	30.28	31.24
n	8	8	34	23	73

through sand in plastic tubes must be slower, and hence the depth of limiting oxygen concentration shallower, than in situ. Further, the 2.5 hour duration of the experiment possibly was too brief for ostracods to attain their optimum depth.

HIPPOMEDON WHERO

A marked and significantly higher mean population density of this amphipod was found in troughs compared with in ripples (Fig. 10.2, Table 10.4). In Aug. 1979 and Mar. 1980 when population densities were lower, these differences were not significant suggesting a possible relationship between total population density and concentration of individuals between ripples. Figure 10.3 reveals that even at low densities more than half of the population occurred in troughs. At greater densities an increasingly larger proportion of the total population occurred in troughs but as the trough density exceeded 220 0.1 m^{-2} and approached 400 0.1 m^{-2}, space apparently became limiting and more individuals occurred in ripples. When the trough density is plotted against total population density (Fig. 10.3B) this phenomenon is equally apparent and the rate of increase in trough density slows above a total density of about 140 0.1 m^{-2}.

This concentration of the population in troughs is apparent in large and

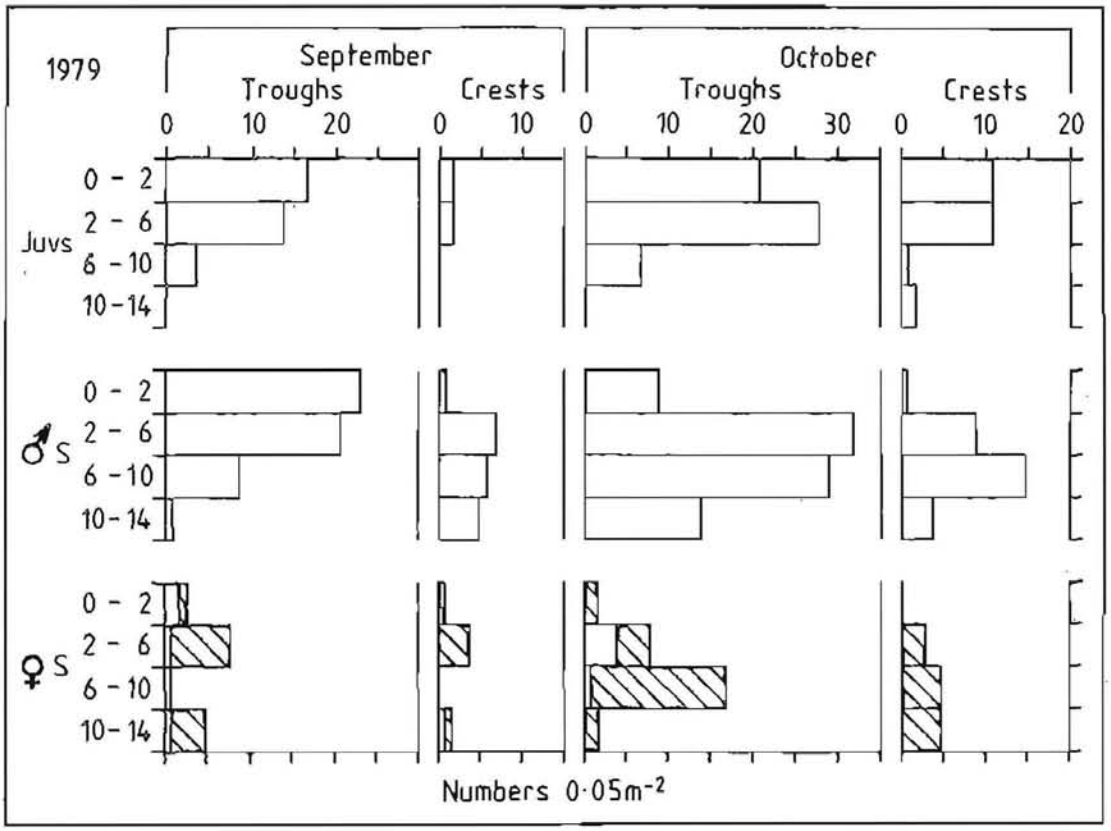

Fig. 10.2 The effect of ripple position on sediment-depth distributions of juvenile, male and female *Hippomedon* (shading, gravid females; sediment depths, cm).

Table 10.4 Differences in mean population densities (nos 0.0125 m^{-2}) of *Hippomedon* with ripple position.

Sample	Troughs $\bar{x}$	Troughs SD	Troughs n	Crests $\bar{x}$	Crests SD	Crests n	t	p
Aug.'79	23.50	10.70	4	9.50	7.416	4	2.151	ns
Sept.'79	27.25	6.801	4	7.50	2.381	4	5.482	<.01
Oct.'79	50.50	9.747	4	22.50	10.472	4	3.914	<.01
Dec.'79	73.0	6.082	3	42.50	21.992	4	2.642	<.05
Mar.'80	18.0	6.055	4	14.5	5.745	4	0.839	ns

Table 10.5 Differences in mean density (nos 0.0125 m^{-2}) of juvenile, male and female *Hippomedon* with ripple position. Data for Aug., Sept., Oct. (and Dec. for females) 1979 and Mar. 1980 pooled.

	Juveniles		Males		Females	
	Troughs	Crests	Troughs	Crests	Troughs	Crests
$\bar{x}$	7.25	3.188	15.0	6.375	7.211	3.737
SD	6.588	4.199	7.668	4.395	3.924	2.579
n	16	16	16	16	19	19
t	2.080		3.903		3.225	
p	<.05		<.001		<.01	

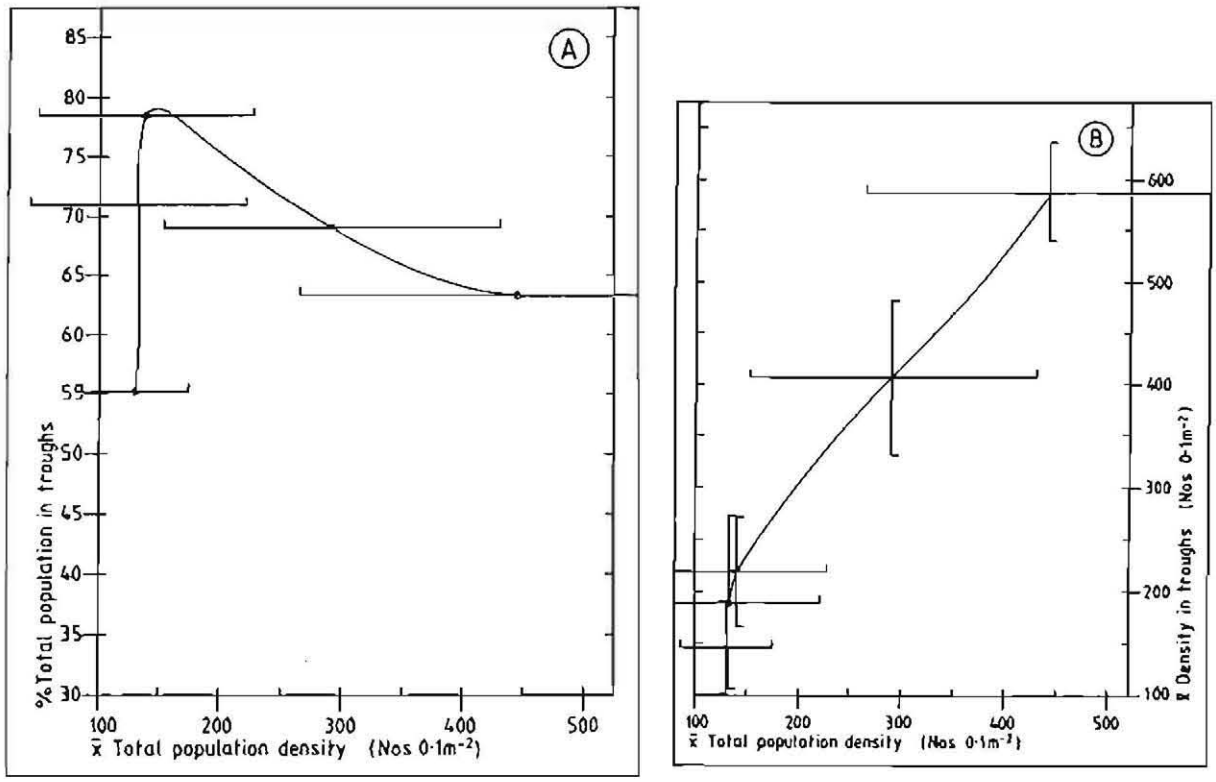

Fig. 10.3 The effect of changes in the total *Hippomedon* population density on the percentage of the population inhabiting troughs (A) and on the mean density of individuals in troughs (B) (vertical and horizontal bars show 95% confidence limits).

small individuals and in both sexes (Table 10.5) indicating an avoidance of ripples and a preference for the trough habitats. Analysis of the depth frequency data for Sept. - Oct. 1979 by anova confirms these findings (Appendix 6.3): The effect of ripple position on frequency is significant ($p < .01$) as is the effect of time on frequency ($p < .05$). Also, as expected, frequency was dependent on both sex and sediment depth alone. Further, the sediment-depth frequency was dependent upon ripple position and upon the sex of individuals in question ($p < .05$ in both cases).

Examination of the mean depths inhabited by juveniles, males and females with ripple position and with time (Table 10.6) illustrates some of these effects. Juveniles inhabited a mean depth of 33.03 mm with no significant

Table 10.6 Mean sediment depths inhabited by significantly different (see Appendix 6.4) groups of juveniles, male and female *Hippomedon*.

		Depth (mm)		
		$\bar{x}$	SD	n
Juveniles		33.03	24.66	122
Males	Sept. troughs	35.37	27.59	54
	crests	72.11	35.68	19
	Oct.	65.66	32.76	113
Females	Sept.	60.0	41.91	24
	Oct. troughs	64.17	29.33	24
	crests	90.0	30.15	12

differences attributable to time or to ripple position (Appendix 6.4). During Sept. males were found at a considerably shallower mean depth between ripples than on ripples, but there was no such difference in Oct. (Table 10.6). The mean depth occupied by males in Oct. (65.66 mm) was significantly different from their Sept. trough mean depth (35.37 mm), but not different from their Sept. mean depth in ripples (72.11 mm). No differences were detected for mean depths inhabited by gravid females either with ripple position or with time, and their overall mean depth (72.50 mm, SD = 34.86, n = 48) did not differ significantly from depths occupied by other females. For total females there was no significant difference in mean depth inhabited with ripple position during Sept. (60.00 mm), but the difference between troughs and on ripples was significant in Oct. (64.17 mm and 90.00 mm respectively).

Further t-tests on these data (Table 10.6) showed significant differences in the mean depths inhabited by juveniles, males and females of each group (Appendix 6.4). The mean depth inhabited by juveniles was significantly ($p < .01$) shallower than depths occupied by males and females except the mean depth for males from troughs in Sept. was not significantly different. Male and female

comparisons are more complicated. Total females for Sept. were significantly deeper than Sept. males between ripples and not significantly different from Sept. males in ripples. Females in troughs during Oct. occurred significantly deeper than males found in troughs in Sept., but their mean depth did not differ significantly from that of the total males in Oct. There was no significant difference in mean depth in ripples for Sept. males and Oct. females, but in Oct. females in ripples dwelt significantly deeper than the total males for that month.

These data then indicate complex relationships between juvenile, male and female density, time, ripple position and sediment-depth distribution. Males, females and juveniles were more abundant between ripples except at extreme densities and optimum sediment depths were apparent for trough and crest habitats although not always realised for males and females. A variety of other factors must be important in modifying spatial arrangement of each group of the population in each subhabitat. These will include abiotic factors such as disturbance and oxygen concentrations, and, perhaps more importantly, biotic factors such as intra- and interspecific competition, predators and food supply.

PATUKI ROPERI

Although there were significant differences in total population mean density with ripple position in Aug. 1979 and Mar. 1980 but not during Sept., Oct. and Dec. 1979 (Table 10.7), further analysis of these data shows that overall, juveniles, males and females were distributed independently of ripple position (Table 10.8, Fig. 10.4). An analysis of variance of the data for Sept. - Oct. 1979 (Appendix 6.5) indicates that the frequency of each sex (including juveniles) was independent of ripple position alone, but depended on ripple position and time. Since frequency changed significantly with time, then a change in the proportion of the population dwelling between ripples may occur with density or with change in the population structure. Such changes in the proportion of the population found in troughs did occur, but these were not directly related to the between-ripple (trough) density nor to the total population density.

The anova also showed that the frequency of individuals changed significantly with depth and that their depth distribution was dependent upon individual status and ripple position together, but not ripple position alone. An analysis of the mean sediment depths inhabited by juveniles, males and females (Appendix

Table 10.7 Differences in mean population densities (nos 0.0125 m^{-2}) of *Patuki* with ripple position at different times.

Sample	Troughs $\bar{x}$	Troughs SD	Troughs n	Crests $\bar{x}$	Crests SD	Crests n	Significance t	Significance p
Aug.'79	26.50	9.983	4	11.25	2.50	4	2.964	<.05
Sept.'79	17.50	5.802	4	12.75	8.016	4	0.960	ns
Oct.'79	33.25	6.850	4	37.75	9.535	4	0.767	ns
Dec.'79	45.333	18.824	3	31.5	23.756	4	0.814	ns
Mar.'80	12.0	2.0	4	6.75	2.754	4	3.085	<.05

Table 10.8 Differences in mean density (nos 0.0125 m^{-2}) of juvenile, male and female *Patuki* with ripple position. Data for Aug., Sept., Oct., Dec. 1979 and Mar. 1980 pooled.

	Juveniles		Males		Females	
	Troughs	Crests	Troughs	Crests	Trough	Crests
$\bar{x}$	11.778	7.833	7.444	8.611	6.278	5.0
SD	11.415	9.883	4.756	6.921	4.012	3.614
n	18	18	18	18	18	18
t	1.109		0.590		1.004	
p	ns		ns		ns	

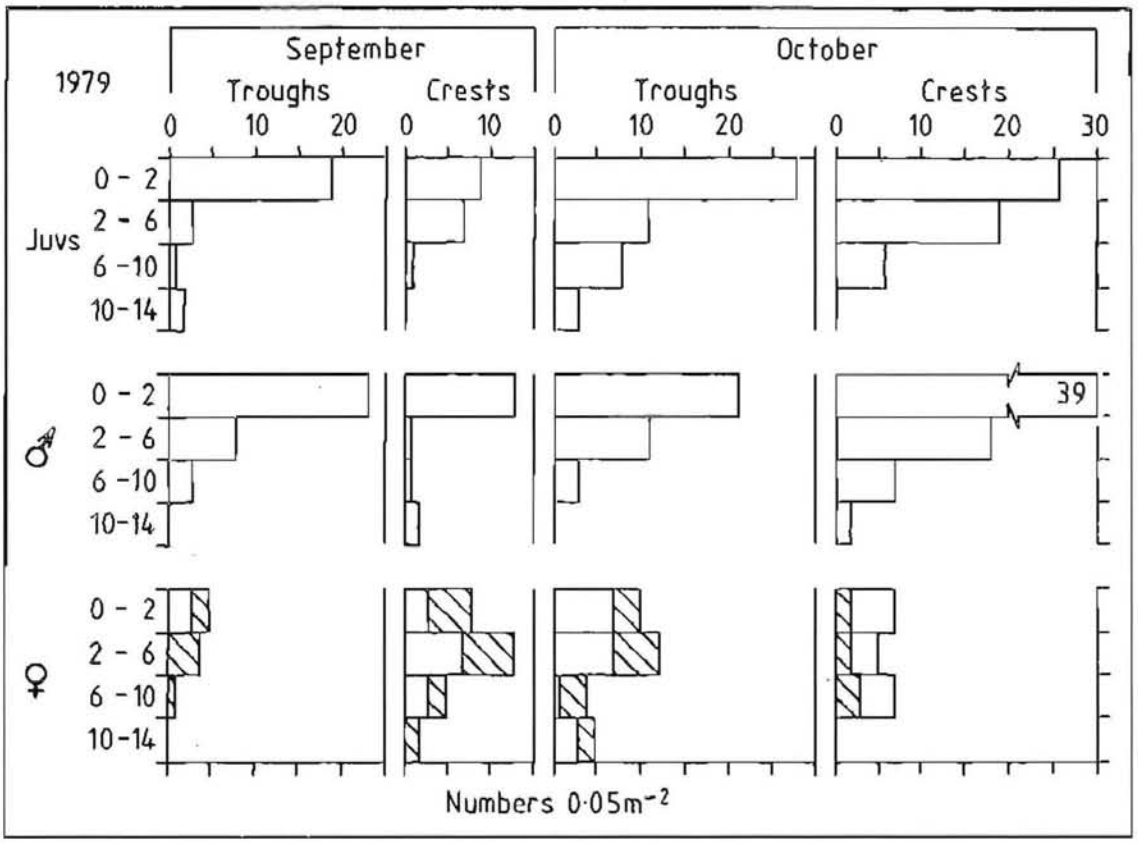

Fig. 10.4 The effect of ripple position on sediment-depth distributions of juvenile, male and female *Patuki* (shading, gravid females; sediment depths, cm).

6.6) summarisedin Table 10.9 showed no significant differences in depth distribution with ripple position, and indeed detected no significant differences in mean depth within each sex group. Further tests (Table 10.9) found no significant difference between the mean depths occupied by juveniles and males but showed that females lived significantly deeper than males or juveniles.

Table 10.9 Mean sediment depths inhabited by juvenile, male and female *Patuki* (data from Sept. - Oct. 1979) (see also Appendix 6.6).

	Depth (mm)			
	$\bar{x}$	SD	n	
Juveniles	26.01	23.14	143	t = 0.526, ns
Males	27.57	27.76	153	t = 4.394, p<.001
Females	43.86	33.51	88	t = 3.861, p<.001

METAPHOXUS LITTORALIS

The mean total population densities of this amphipod did not differ significantly with ripple position (Table 10.10) except in Mar. 1980. Figure 10.5 shows however, that both males and females were more abundant on ripples than between ripples, but there was no such difference in juveniles abundance (Table 10.11). Anova analysis of data for Sept. - Oct. 1979 demonstrates the importance of ripple position alone and with sexual status in the species distribution pattern (Appendix 6.7). In addition, the frequency of juveniles, males and females in either ripple position was dependent upon time.

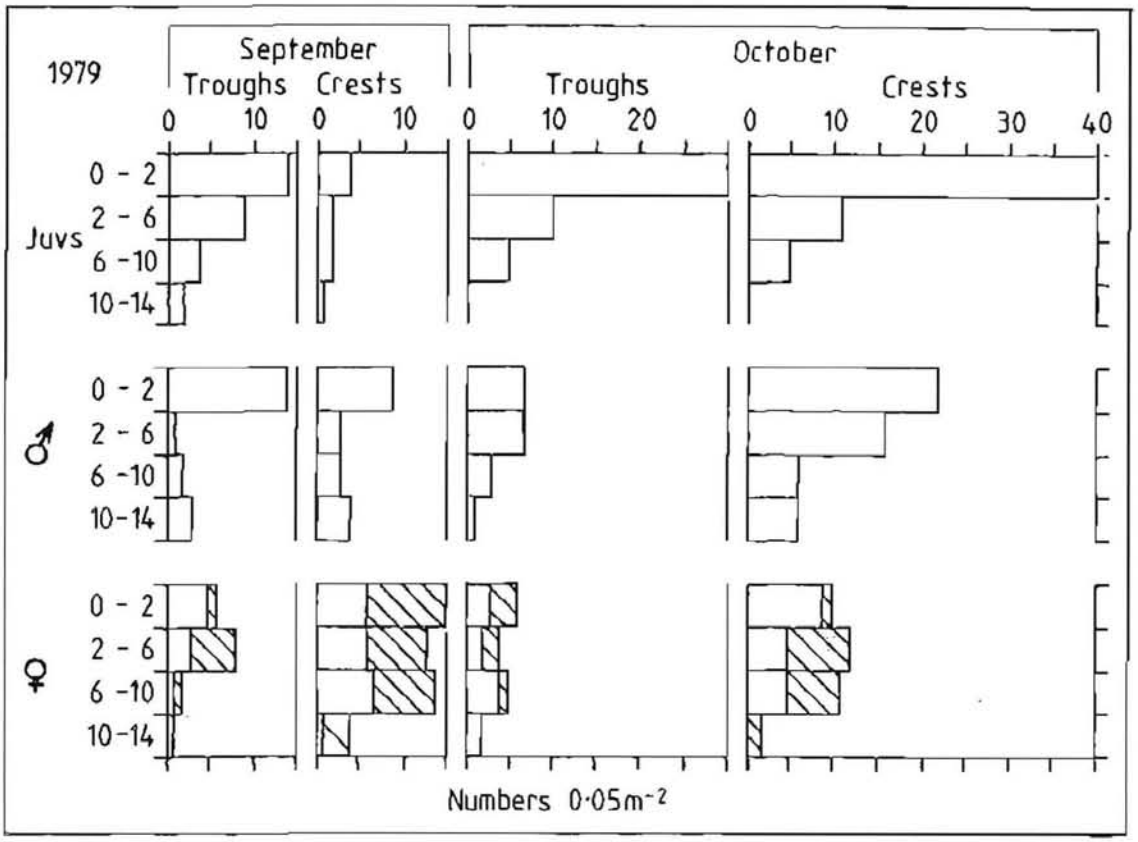

Fig. 10.5 The effect of ripple position on sediment-depth distributions of juvenile, male and female *Metaphoxus* (shading, gravid females; sediment depths, cm).

The Anova also demonstrated the relationships between frequency and depth inhabited with respect to sexual status, time and ripple position. There was a significant relationship between frequency and sediment depth, but the depth-

frequency was independent of ripple position. Further, there were significant interactions of the depth frequency with time and sexual status separately and together.

These interactions of depth-frequency were investigated by comparing mean depths inhabited by juveniles, males and females between and on ripples in Sept. - Oct. 1979 (Appendix 6.8, Table 10.12). In all cases there was no significant difference in mean depth with ripple position and only juveniles were at significantly different depths at different times. Males and females were found at similar (not significantly different) mean depths which were significantly different from the juvenile Oct. mean depth but not different from the juvenile Sept. mean depth (Table 10.12).

Thus *Metaphoxus* males and females inhabited similar depths at both times and ripple positions but were more abundant in ripples, whereas juvenile density was independent of ripple position but their shallower dwelling depth changed with time.

Table 10.10 Differences in mean population densities (nos 0.0125 m^{-2}) of *Metaphoxus* with ripple position at different times.

Sample	Troughs $\bar{x}$	Troughs SD	Troughs n	Crests $\bar{x}$	Crests SD	Crests n	Significance t	Significance p
Aug.'79	15.25	5.620	4	12.75	4.992	4	0.665	ns
Sept.'79	16.50	6.758	4	19.50	4.509	4	0.739	ns
Oct.'79	27.25	15.861	4	40.25	8.846	4	1.432	ns
Dec.'79	60.0	11.358	3	43.75	17.328	4	1.398	ns
Mar.'80	12.25	6.551	4	30.75	8.617	4	3.418	<.05

Table 10.11 Differences in mean density (nos 0.0125 m^{-2}) of juvenile, male and female *Metaphoxus* with ripple position. Data for Aug., Sept., Oct. 1979 and Mar. 1980 pooled.

	Juveniles		Males		Females	
	Troughs	Crests	Troughs	Crests	Troughs	Crests
$\bar{x}$	6.25	5.785	4.938	9.25	6.438	10.625
SD	7.733	7.274	3.193	5.385	3.444	6.109
n	16	16	16	16	16	16
t	0.053		2.755		2.388	
p	ns		<.01		<.05	

Table 10.12 Mean sediment depths inhabited by juvenile, male and female *Metaphoxus* (data for Sept. - Oct. 1979) (see also Appendix 6.8).

	Depth (mm)			Significance
	$\bar{x}$	SD	n	t,p
Juveniles				
Sept.	38.42	34.84	38	2.509, <.05
Oct.	23.17	22.45	101	
Males	41.12	38.69	107	1.408, ns
Females	48.07	34.41	114	

Juveniles (Sept.) vs Juveniles (Oct.): 0.391, ns
Juveniles (Sept.) vs Males: 4.120, <.001
Juveniles (Sept.) vs Females: 6.350, <.001
Juveniles (Oct.) vs Males: 1.483, ns

Table 10.13 Differences in mean population densities (nos 0.0125 m^{-2}) of *Paraphoxus* with ripple position at different times.

Sample	Troughs $\bar{x}$	Troughs SD	Troughs n	Crests $\bar{x}$	Crests SD	Crests n	Significance t	Significance p
Aug.'79	0.75	0.957	4	2.25	1.258	4	1.898	ns
Sept.'79	3.25	1.50	4	3.75	2.50	4	0.343	ns
Oct.'79	4.50	3.416	4	16.25	11.955	4	1.890	ns
Dec.'79	21.0	1.0	3	13.0	8.544	4	1.624	ns
Mar.'80	3.50	3.109	4	10.25	4.272	4	2.555	<.05
Aug.'80	4.5	1.915	4	3.25	0.50	4	1.263	ns
Oct.'80	20.75	14.795	4	12.50	5.916	4	1.025	ns

Table 10.14 Differences in mean density (nos 0.0125 m^{-2}) of juvenile, male and female *Paraphoxus* with ripple position. Data for Aug., Sept., Oct., Dec. 1979 and Mar., Aug., Oct. 1980 pooled.

	Juveniles		Males		Females	
	Troughs	Crests	Troughs	Crests	Troughs	Crests
$\bar{x}$	6.148	5.857	0.630	0.929	1.074	1.786
SD	9.658	7.049	0.967	0.716	1.357	1.595
n	27	28	27	28	27	28
t	0.127		1.300		1.785	
p	ns		ns		ns	

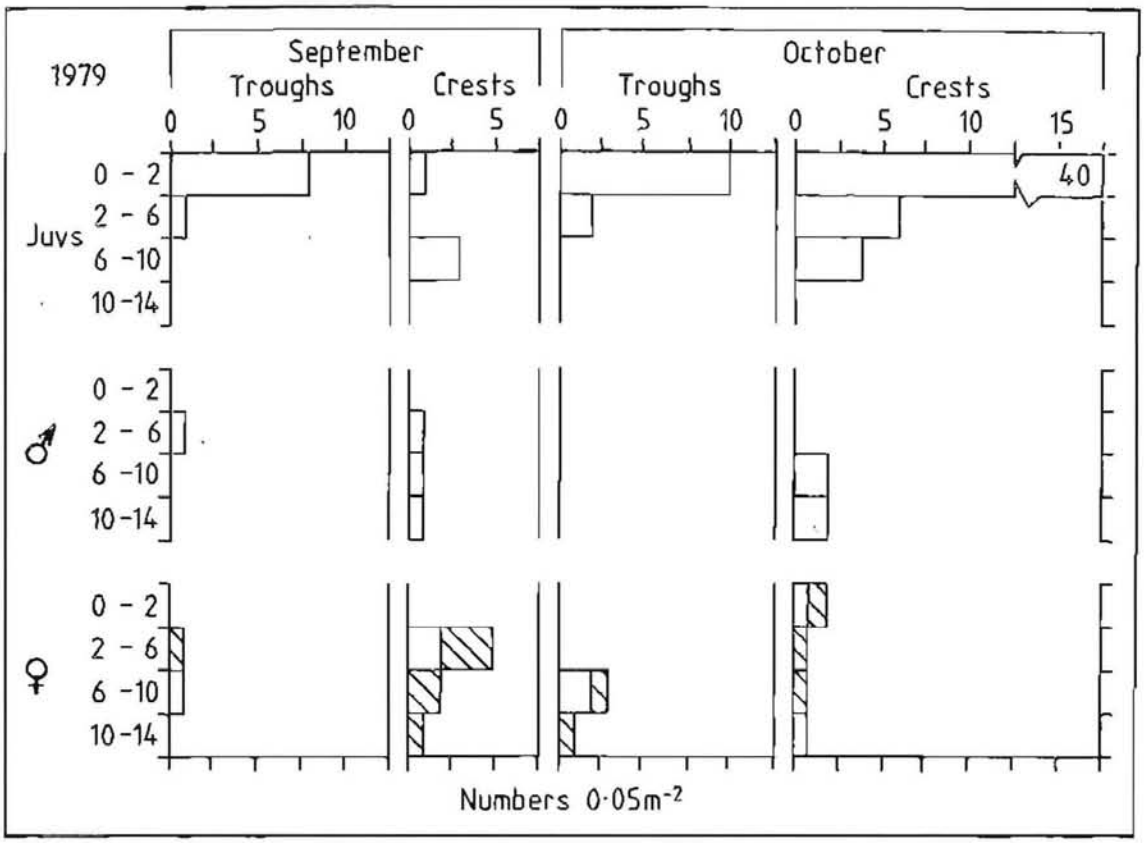

Fig. 10.6 The effect of ripple position on sediment-depth distributions of juvenile, male and female *Paraphoxus* (shading, gravid females; sediment depths, cm).

Table 10.15 Mean sediment depths inhabited by juvenile, male and female *Paraphoxus* (data for Sept. - Oct. 1979) (see also Appendix 6.10).

	Juveniles			Males	Females
	Sept.				
Depth (mm)	Troughs	Crests	Oct.		
$\bar{x}$	13.33	62.50	18.39	85.0	64.21
SD	10.0	35.0	19.18	33.38	34.21
n	9	4	62	8	19
t \ p					
juveniles					
Sept. between		<.05	ns	<.001	<.001
on	2.760		<.05	ns	ns
Oct.	1.226	2.497		<.001	<.001
males	5.844	1.066	5.528		ns
females	5.967	0.089	5.576	1.467	

PARAPHOXUS AUSTRALIS

Data for this amphipod are less reliable than for the others because its generally lower density resulted in few individuals being collected at any time. It was however, studied over a longer period and in only one of seven times was there any significant difference in mean total population density with ripple position (Table 10.13). When these data were pooled, there was no significant effect of ripple position on the densities of juveniles, males or females (Table 10.14).

The analysis of variance on the *Paraphoxus* data for Sept. - Oct. 1979 (Appendix 6.9) did however, indicate that ripple position alone had a significant influence on density. In both months the total population mean density was higher on ripples than in troughs as were the mean densities of males and females (Fig. 10.6). The anova also showed a significant interaction between frequency and sex, and that sediment-depth frequencies were dependent upon sexual status.

There was no difference in mean depth inhabited with time or ripple position for either males or females (Table 10.15), but the mean depth of occurrence for juveniles differed with ripple position in Sept. and with time. Juveniles dwelt at significantly shallower depths than males or females (except for the Sept. in ripple samples) and, although the mean depth of habitation for males was deeper than for females, this was not significant.

COMPARISON OF SPECIES DISTRIBUTIONS

Figure 10.7 compares the mean depths (± 1SE) of occurrence in the sediment for all significantly different species subgroups for juveniles, males and females of all species (in *Cycloleberis* sexes were not separated for this analysis but instars constitute the subgroups). There is considerable overlap in their vertical ranges, especially when the standard errors are considered. Definite patterns are apparent when mean depths are examined closely. *Cycloleberis* obviously dominates deeper strata, whereas *Patuki* occurs almost exclusively shallower than 45 mm. Further, the *Patuki* population is separated into juveniles and males at mean depths of 26 and 27.5 mm respectively, and females at 43.5 mm depth. *Metaphoxus* overlaps considerably with *Patuki*, but of the *Metaphoxus* population, only Oct. juveniles occurred at a mean depth of less

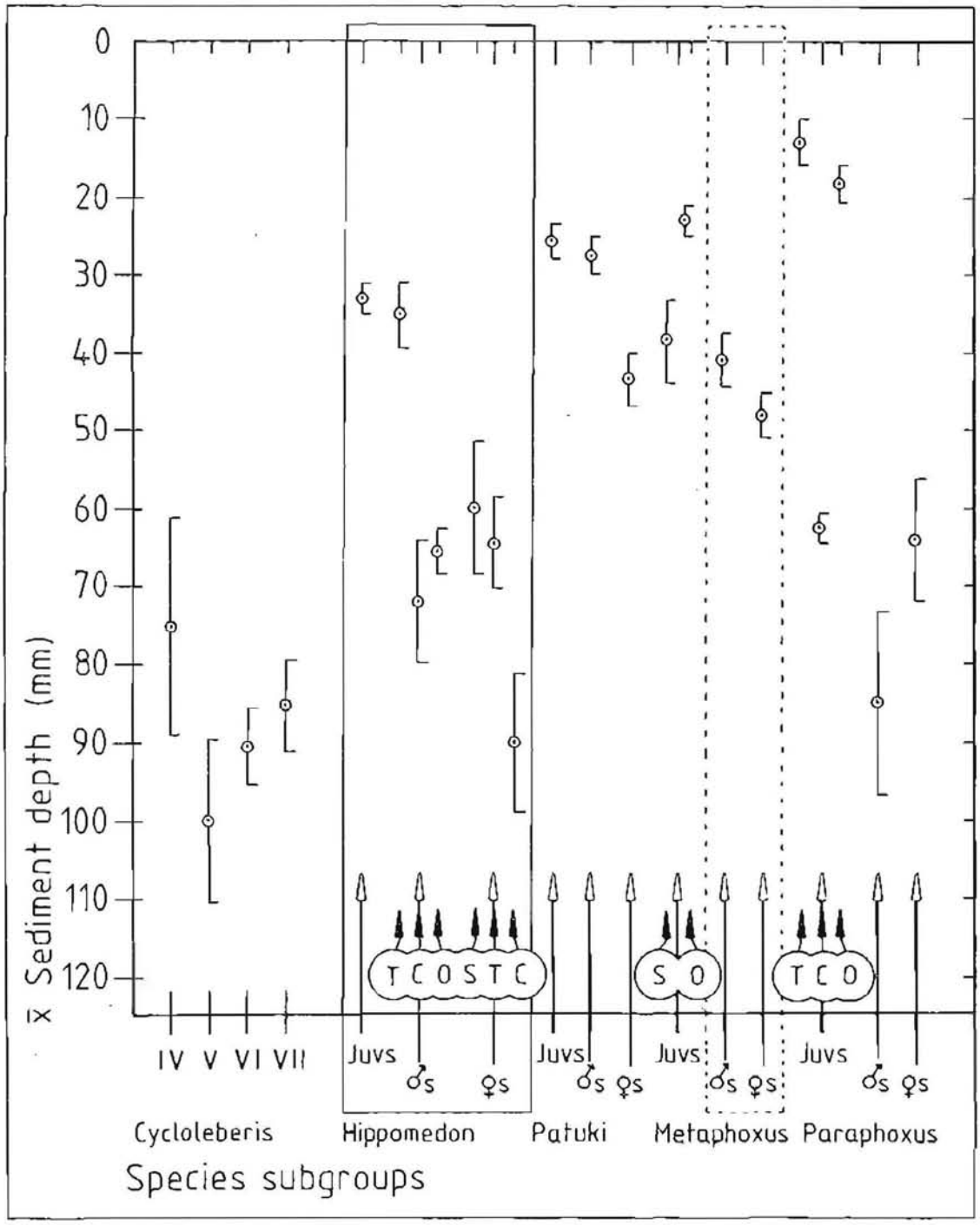

Fig. 10.7 Mean (± ISE) sediment depths inhabited by significantly different species subgroups (solid bracket, more abundant in troughs; broken bracket, more abundant in crests; S, September; O, October; T, troughs; C, crests).

than 35 mm. Although the depth distribution of *Hippomedon* overlapped considerably with that of *Metaphoxus*, the actual overlap was much less because the *Hippomedon* population was concentrated between ripples, whereas *Metaphoxus* males and females were concentrated within ripples. Where there were significant differences in mean depth of occurrence with ripple position, *Hippomedon* was found at shallower depths between ripples and deeper in ripples. *Paraphoxus* was more abundant in ripples where its mean depths of occurrence were deeper than those of *Metaphoxus* except that at times the mean depths of juveniles were shallower than the shallowest *Metaphoxus*.

In view of the differences in mean depths inhabited by the various species subgroups and their resultant susceptibilities to displacement from the sediment, attempts were made to record individual burrowing rates for each species. It proved impossible to record rates for individuals of known subgroups (sex) and specimens of *Metaphoxus* were extremely difficult to isolate and observe. No individuals of *Paraphoxus* were available at the time of making these observations.

Instars V and VI of *Cycloleberis* burrowed at similar rates and an average took 11.2 s to disappear beneath the sediment (Table 10.6). Their mean burrowing rate was signficantly faster than for instar VII females and males which took 17.0 and 24.1 s respectively. Adult *Hippomedon* burrowed beneath the sediment in a mean time of 4.3 s (SD = 2.4, n = 40) while individuals of *Patuki* took about 0.5 s, (n = 8), a time too brief for accurate measurement by stopwatch. Three individuals of *Metaphoxus* provided a mean burrowing time of 4.1 s (SD = 5.110, n = 3) ranging from 1.1 to 10.0 s.

There is distinct tendency for faster burrowers to live near the sediment surface and for slower burrowers to live deeper in the sediment when the above rates are compared with mean depths inhabited by adults of each species (Fig. 10.7). *Patuki*, the fastest burrower, had an adult mean depth of about 35 mm but observations in situ and in the lab. showed that it lives within the surface 15 mm, and that it leaves the sediment frequently to swim rapidly just above the sand for short distances before re-entering. Individuals usually burrowed with the body axis parallel to the sediment surface and penetrated only shallowly so that the cryptically-coloured dorsal surface and red eye were visible. When disturbed however, they burrowed below the surface and were capable of moving about with ease while covered, apparently continuing to move

Table 10.16 Burrowing rates of *Cycloleberis* instars V - VII in the laboratory.

Instar	Burrowing Rate(s) $\bar{x}$	SD	n	Significance t	p
V	11.1	1.8	12		
				0.170	ns
VI	11.3	3.5	30		
V - VI	11.2	3.1	42		
				2.619	<.01
VII ♀	17.0	8.9	18		
				2.324	<.05
VII ♂	24.1	7.7	12		

ventral first by displacing sediment dorso-laterally with shuffling movements of peraeopods 3 - 6. The mean depths of occurrence for *Patuki* thus probably are too deep and result from their burrowing escape response to sampling.

DISCUSSION

Within the South Bay shelly sand habitat the depth distribution of the crustaceans probably results from their responses to several factors. Most probably burrow to escape predation by the various fishes present, and they must either burrow to a sufficient depth to avoid being uncovered by wave-induced sediment movement, or continually alter their position before being washed from the sand. A compromise between the two probably operates for most individuals. The maximum depth of habitation will be limited by the oxygen concentration of interstitial water and by the availability of suitable food, while the minimum depth may be determined by the probability of displacement from the sediment and subsequent predation, and by the energy required to maintain their optimal depth situation. Having established the balance

between these constraints, the animals must then contend with alteration of their dwelling depth by the horizontal migration of sand ripples, usually 15 - 20 cm from trough to crest. Ripple migration however, usually must be very slow relative to the high in-sediment mobility of all species, even the slowest burrower *Cycloleberis*. Thus under normal sea conditions their burrowing abilities must enable them to relocate a favourable position with ease whenever adverse conditions develop. The relationship between mean dwelling depth and burrowing rate described above however, must reflect the probability of displacement from the sediment, probably during storms, when fast-burrowing surface-dwellers (e.g. *Patuki*) are continually displaced but slower, deeper burrowers (e.g. *Cycloleberis*) are more rarely washed from the sand.

As seen in Fig. 10.7 there is considerable overlap in the sediment-depth ranges of species and species subgroups. Therefore, having identified these significantly different groups, it seems useful to examine their degree of overlap or the intensity of use of the sediment profile. Since space is one of the three components of niche (Pianka, 1970b), it seems appropriate to use an index of niche overlap for this purpose.

Several measures of niche overlap have been proposed with much discussion of their individual merits and failings (reviewed by Hurlbert, 1978 and Linton *et al*, 1981 which continues (Hurlbert, 1982)). Despite their various shortcomings, a range of indicies continue to be used and Linton *et al*. (1981) recently provided an excellent demonstration of the effectivenesses of four indicies. Among these Schoener's (1970) index proved most accurate, especially with a sample size greater than 16 per resource, although it progressively under-estimated overlap as true overlap increased above 0.76. Within 0.85 - 0.90 overlap, Schoener's index was no less accurate than the others but at overlaps greater than 0.90 it was less accurate than the other three indicies. Schoener's index then, proved most reliable overall and it seems excellent for the purpose of this study. The index is defined as:

$$C_{ik} = 1 - \tfrac{1}{2}\Sigma|p_{ij} - p_{kj}|$$

where $p_{ij} = N_{ij}/Y_i$, the proportion of individuals of species subgroup i associated with resource state j, and $p_{kj} = N_{kj}/Y_k$, where k is the remaining subgroups of the same species or for community overlap, the remaining subgroups of all species.

Application of the index in this way provided the measures of intra and interspecific subgroup habitat partitioning listed in Table 10.17. Values for *Paraphoxus* are questionable because of the low numbers (mostly less than 16 per layer for pooled data) of individuals in the sectioned cores. When the overlap of each species subgroup is plotted against the subgroup's mean depth of occurrence (Fig. 10.8), there is a marked peak in proportional overlap at about 40 mm sediment depth, indicating that competition for space is greatest at this depth. Above and below the 40 mm level the proportional overlap declines in a linear manner to lowest values deeper in the sediment. Figure 10.9 demonstrates the linear nature of this relationship between proportional overlap and distance from the optimum 40 mm depth sediment layer, which is described by the regression equation $Y = 0.859 + -0.0085X$ ($r = -0.873$, $p < 0.01$). Thus for most species subgroups the 40 mm level appears to be the optimum physically, chemically and biologically except for competition. Obviously competition must be most intense at this depth and the competitive abilities of each species subgroup largely determine their mean depths of occurrence relative to this.

Juveniles predominated near the sediment surface and only juvenile *Paraphoxus* living within ripples had a mean depth greater than the 40 mm level. Presumably juveniles are better able to compete with other juveniles than with adults and so inhabit these upper layers to avoid competition with adults. It was impractical to compare burrowing abilities of juveniles with adults because of the small sizes of juveniles, but there is no reason to believe the adults are better burrowers. The sand was uncompacted, coarse, and well sorted (see Chapter 3) and the large interstitial spaces may mean that small individuals could move through the sediment with little effort. Apart from juveniles, only male *Patuki* and male *Hippomedon* (troughs) had mean depths of occurrence shallower than 40 mm. Females of all species subgroups had mean depths of occurrence below 40 mm, presumably where the sediment was more stable.

Several workers have reported that intertidal amphipods are most abundant in the surface 40 - 50 mm of sand (Croker, 1967; Sameoto, 1969). Oliver *et al.* (1980) found that 85.2% of the Crustacea at their 9 m depth station occupied the 0 - 50 mm layer. Sediments at that station were considerably finer than in South Bay (3.27 ø cf 1.14 - 1.65 ø) and, because water flow through such sediments and consequently reoxygenation would be slower, the optimum dwelling depth probably was shallower than 40 mm. Croker & Hatfield (1980) found that

Table 10.17 Proportional niche overlap for each significantly different (Fig. 10.7) species subgroup with (a) the remaining subgroups of the same species and (b) with the other four species and the remaining subgroups of the species in question.

Species subgroup	Proportional overlap (a) Within species	(b) Remaining subgroups
Cycloleberis		
instar IV	0.685	0.525
V	0.775	0.398
VI	0.920	0.438
VII	0.885	0.485
Hippomedon		
juveniles	0.657	0.830
males Sept. between	0.888	0.859
on	0.603	0.700
Oct.	0.743	0.681
females Sept.	0.680	0.613
Oct. between	0.757	0.701
on	0.642	0.468
Patuki		
juveniles	0.966	0.672
males	0.845	0.753
females	0.744	0.908
Metaphoxus		
juveniles Sept.	0.930	0.753
Oct.	0.646	0.642
males	0.707	0.928
females	0.766	0.884
Paraphoxus		
juveniles Sept. between	0.111	0.578
on	0.273	0.454
Oct.	0.295	0.574
males	0.351	0.524
females	0.394	0.686

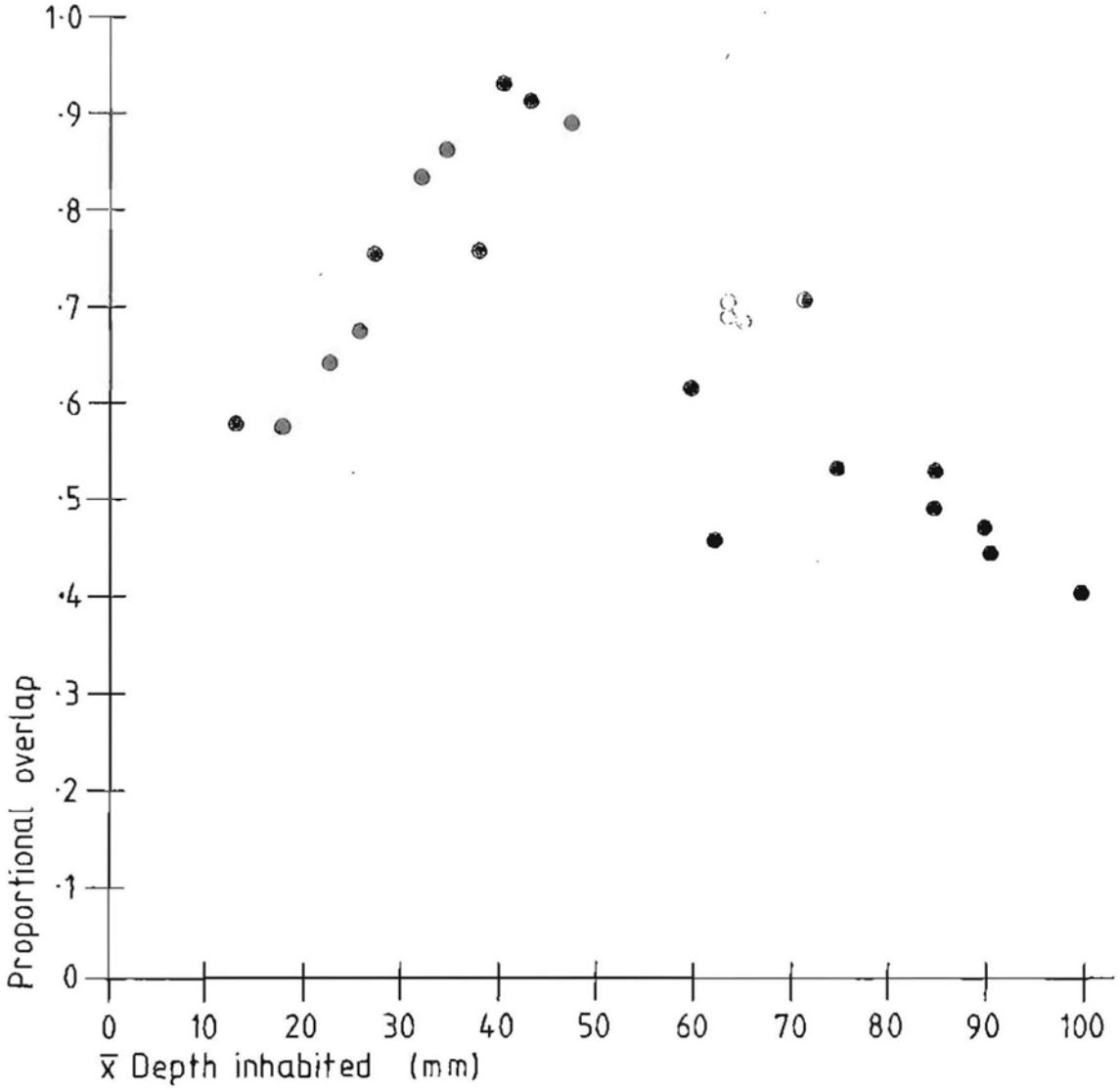

Fig. 10.8 Changes in the proportional overlap of each species subgroup with mean depth inhabited.

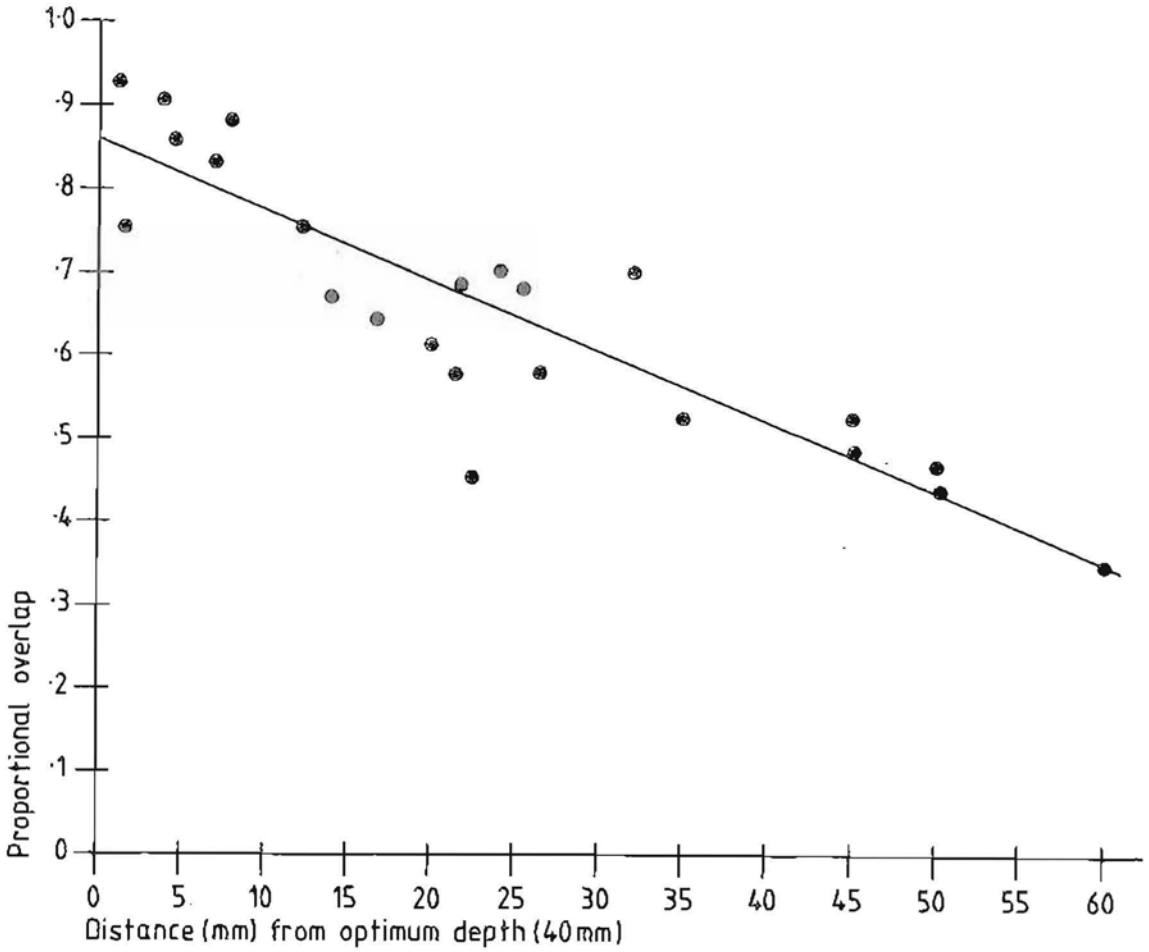

Fig. 10.9 Relationship between proportional niche overlap and distance from the optimum sediment depth (40 mm).

amphipods *Amphiporeia virginiana*, *Haustorius canadensis* and *Acanthohaustorius millsi* exhibited definite sediment-depth preferences within the 0 - 100+mm layer, and that these varied with sexual maturity, reproductive status, season, beach level (position relative to mean low water) and with the abundance of other species. Despite species preferences for different beach levels and sediment depths, there was considerable overlap by all species at most times. As in the present study, juveniles increased space partitioning by inhabiting shallower sediment depths within their species preferred beach zone (Croker & Hatfield, 1980). In his elaborate studies on two intertidal haustoriids, Grant (1981a,b) showed distinct vertical segregation imposed by *Acanthohaustorius millsi*, the stronger competitor, displacing *Pseudohaustorius caroliniensis* into

deeper (and often reducing) sediment layers. Similarly, *Bathyporeia sarsi* displaced its sibling *B. pilosa* to slightly deeper layers, and the presence of the latter resulted in *B. sarsi* occurring slightly closer to the sand surface than when alone (Nicolaisen & Kanneworff, 1969). In both cases however, there was considerable vertical overlap within each species pair.

The present study detected significant differences in the abundances of some species with ripple position showing that the habitat was partitioned both horizontally and vertically. Partitioning in both dimensions probably results from competitive interactions, the availability of various food resources and a suite of abiotic factors. Eckman (1979) hypothesized that differences in flow patterns and velocities at various points over rippled sediment would affect the distribution of smaller macrobenthic animals both directly and indirectly. Hogue & Miller (1981) demonstrated that intertidal nematodes were concentrated within ripples and postulated that differences in water flow over the ripples was indirectly responsible: Organic and faecal material was concentrated in troughs and subsequently buried by advancing ripples where it became available to infaunal nematodes. A similar situation may ensue in South Bay. Usually no layer of organic material was apparent in cores but allochthonous plant debris seemed scattered throughout the sand profile. Certainly there were often accumulations of plant debris in troughs and on a few occasions a black, anoxic layer of organic debris was obvious between 120 - 160 mm depth. Anoxic layers were not present in the sectioned cores and no records of organic matter were made.

Any direct effects of water flow differences over ripples would most likely influence the distribution of surface and shallow dwellers. In South Bay *Patuki*, a very active surface dweller, was similarly abundant both on ripples and in troughs. Casual observations of its behaviour, examination of the crop contents of a few individuals and of faecal material indicate that it browsed on sand epiphyton and microflora, and that it was not inconvenienced by normal swell conditions and flow velocities over ripples. *Metaphoxus* (males and females) and *Paraphoxus* however, both active, shallow burrowers, were significantly more abundant within ripples than in troughs. Oliver *et al.* (1982) reported that various phoxocephalid amphipods, including *Paraphoxus* sp. (probably *P. australis*) from Kaikoura, consumed a variety of small infaunal invertebrates, including nematodes, and diatoms. My examinations of the crop contents confirm that both phoxocephalids are predaceous and *Metaphoxus* in

particular, consumes large numbers of harpacticoid copepods. Thus the greater abundance of these two amphipods within ripples may be an indirect effect of water movement. Again, normal sea conditions probably present no problems for these two and if, as Hogue & Miller (1981) postulated, organic material buried within ripples attracts meiofauna, then it is not surprising that *Metaphoxus* and *Paraphoxus* also occur at greater densities in ripples.

Hippomedon, another shallow burrower and probably a sandgrain browser because guts examined contained amorphous material and very fine sediment particles, was more abundant in troughs where there would be less competition for space with the two phoxocephalids. Competition with *Patuki*, the other browser, would be minimal because of their different dwelling depths. In addition, the concentration of *Hippomedon* in troughs would reduce its competition for food with the postulated meiofaunal browsers wtihin ripples. The remaining species, *Cycloleberis*, apparently also is a browser since its gut contents closely resembled those of *Patuki*. Its deeper dwelling depth means that it avoids competition with the other browsers (except possibly the meiofauna) regardless of ripple position and that competition for space with the other species is minimal.

Thus the five South Bay macrofaunal crustacean species apparently utilize only two different food sources, but minimize competition by both horizontal and vertical habitat partitioning. Each microhabitat is characterized by a different sediment stability and inherent probability of displacement which is matched by the different burrowing rates of their occupant species.

CHAPTER 11

POPULATION CHANGES OF FIVE CRUSTACEANS RECOLONIZING DEFAUNATED SAND

INTRODUCTION

Rapid colonists of new or underexploited habitats have been called fugitive, colonizing, opportunistic, weedy and r-selected (see Grassle & Grassle, 1974) and they are generally considered to be poor competitors (Hutchinson, 1951; MacArthur & Wilson, 1967; Pianka, 1972). Species inhabiting unstable situations must be capable of rapidly recolonizing areas of the habitat defaunated by catastrophic disturbances for maximum habitat utilization and to capitalize on otherwise unexploited food resources. Thus, high mobility and rapid recolonization of defaunated sand may be an important behavioural adaptation to the South Bay habitat by the five sand-dwelling crustaceans.

Recent work on recolonization of sediment following artificial or natural defaunation has emphasized the reappearance of species, usually by checking at monthly intervals. Work by Sherman & Coull (1980) on recolonization rates of intertidal, estuarine meiobenthos demonstrated remarkably rapid (12 h) recolonization by several species. This study attempts to describe the short-term recolonization of defaunated sand by five species of macrofaunal Crustacea. I also compare the structures of control and recolonized populations to determine which life history stages seem more mobile and then attempt to see how recolonization patterns and recolonizing populations change with time.

METHODS

Recolonization experiments were initiated on 10 Nov. 1979 at one side of the South Bay study area, and continued until 29 May 1980. A full description of the study area was provided in Chapter 3.

Buckets of sand were removed from the margins of the study area and taken to E.P.F.S. where they were drained of sea water, thoroughly washed and stirred in hot (60 - 80°C) tap water twice. The fauna was removed by several sea water washes, agitation and decanting into a sieve until no

further animals were found in the supernatant. Rectangular (0.0576 m^{-2} surface area, 350 mm high) plastic buckets containing fresh sea water were then filled with the sand to within about 50 mm of their tops. Within 40 min. buckets of this defaunated sand were placed in an iron frame on the bottom at the study site. On initiating the experiment on 10 Nov. 1979 eight buckets of sand were put out and held in a single row. The first bucket was retrieved the next day after 24 hours and another one put in its place. Subsequent retrievals and replacements provided recolonization periods of four (10 - 14 Nov.), eight (27 Nov. - 5 Dec.), 16 (10 - 26 Nov.) and 26 days (10 Nov. - 6 Dec.). Buckets were kept upright at all times during recovery. They were enclosed in individual plastic bags on removal from the frame, hoisted to the surface by the boat tender and taken to the lab. where the crustaceans were removed by flotation and decanting (Chapter 2) before preservation in 70% alcohol. Subsequently individuals were sorted to species and counted. Large (> 150 individuals) species samples were divided using a sample splitter to produce one subsample of about 100 individuals each of which was measured, sexed and their reproductive status noted (see Chapter 2 for details). Control samples used here are monthly samples of the populations consisting of three to eight randomly-located 0.0125 m^2 cores taken as described in Chapter 2.

Early in Jan. 1980 severe storms destroyed the experimental frame and buckets. The smashed frame was discovered some 30 m seaward of its original position and without either its anchors or buckets. Thus on 23 Jan. 1980 a single bucket experiment was initiated to monitor recolonization over one night each month and during intervening months. This series was continued until 29 May 1980 producing four over night collections and five one month (26 - 39 days) collections.

RESULTS

Only five species of crustaceans recolonized the defaunated sand in abundance: the myodocopid ostracod *Cycloleberis zealandica* and four amphipods, *Hippomedon whero*, *Patuki roperi*, *Metaphoxus littoralis* and *Paraphoxus australis*. Other recolonists were relatively unimportant and have not been considered further here.

Within 24 hours the density of recolonized individuals exceeded half of the control population density (Fig. 11.1). A slight drop in density occurred about day 4 and thereafter followed a sharp rise to about 800 individuals 0.1 m^{-2} by the eighth day. The density continued to increase

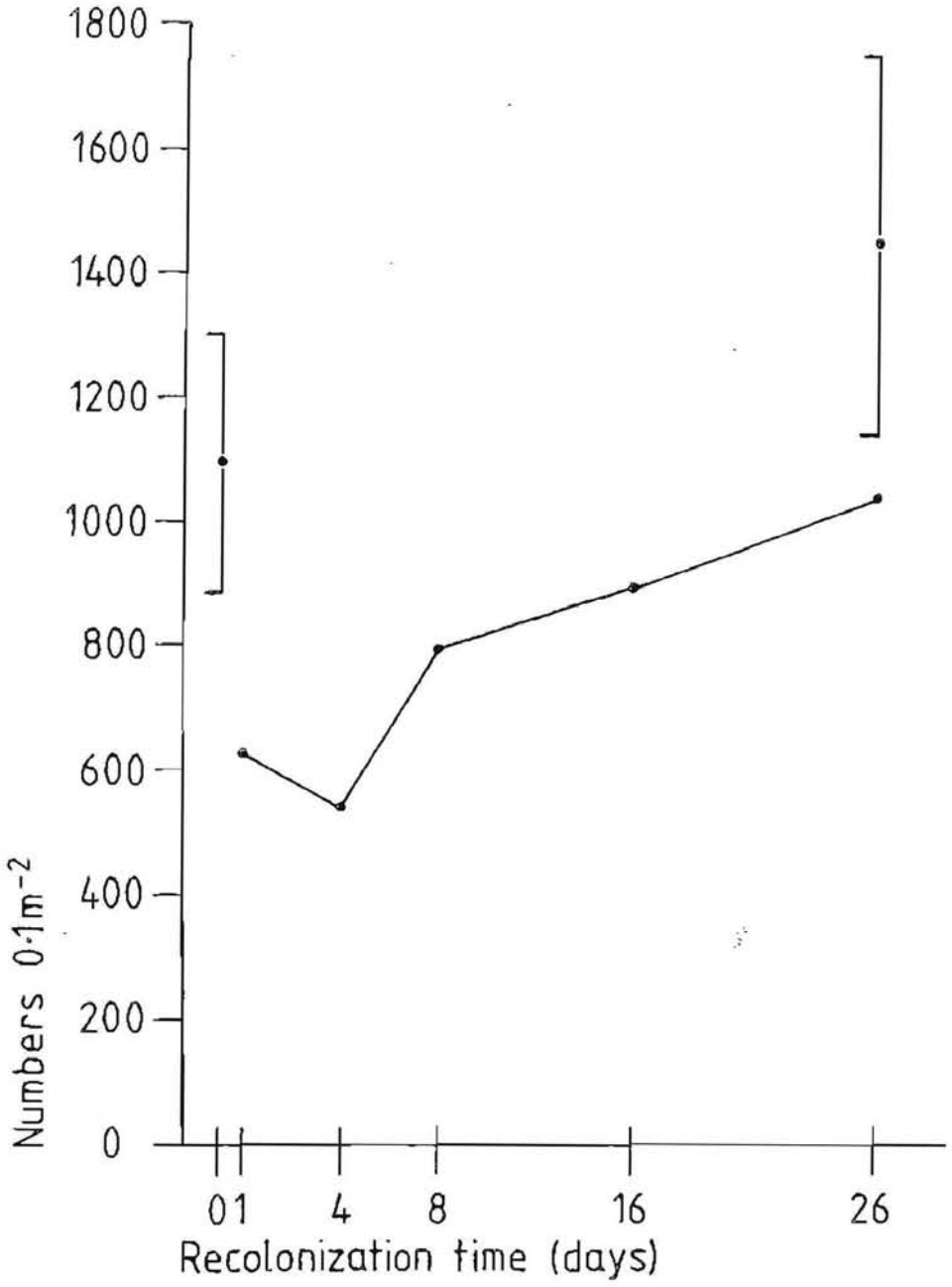

Fig. 11.1 Densities of total fauna in control (closed circles) (mean ± 95% confidence limits) and recolonized populations (open circles).

steadily from day 8 to day 26 when the recolonized population density was about 78% of the control population mean density. Presumably the density of recolonists increased further before the experiment was destroyed by storms in Jan.

Figure 11.2 shows one-day and 26 - 39 day recolonized population densities relative to control population densities between Nov. and May. One-day recolonization was proportionately much less in Jan. and Feb. than in Nov. - Dec. Similarly the 28 - 29 day recolonization was low in Jan. and in May compared with Dec., but it was higher in Mar. and Apr.

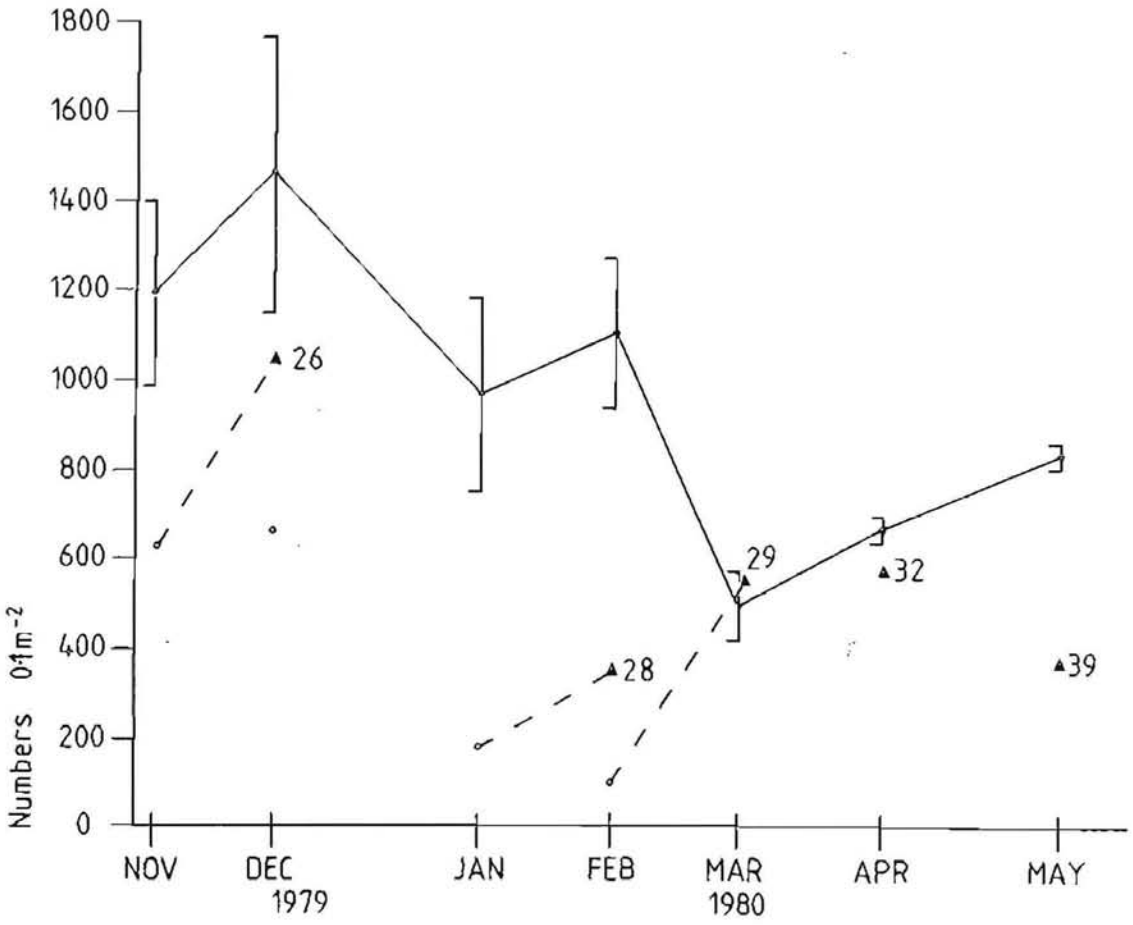

Fig. 11.2 Seasonal differences in densities of total fauna in control population (closed circles) (mean ± 95% confidence limits) and after 1 (open circles) and 26 - 39 (triangles) days recolonization.

CYCLOLEBERIS ZEALANDICA

After just one day the density of recolonized individuals was 5.5 times greater than that of control population (Fig. 11.3) and thereafter it declined sharply to approximate the control population density by the sixteenth day. Table 11.1 shows changes in the structure (instar and sex composition) of the two controls during the experiment and of the recolonized populations with time. Chi square tests (Appendix 7.1) showed that controls were signficantly different ($p < .001$), that recolonized populations differed ($p < .001$) from both controls at all times, and that recolonized populations at successive times differed significantly ($p .001 - < .001$) from each other. Thus it seems that some instars and sexes colonized more rapidly than others and that the population structure had not attained an equilibrium after 26 days.

First instar individuals were the principal early colonists (1 day) and were steadily displaced by later instars, especially IV, V and VI. Within instars IV and V females were the more frequent early colonists (IV, $\chi^2 = 12.653$, $p < .05$; V, $\chi^2 = 29.308$, $p < .001$; dfs = 6), whereas instar VI males colonized more rapidly than did females ($\chi^2 = 25.990$, $p < .001$, dfs = 6). Adult females were the slowest instar to recolonize and, although numbers were low, gravid females apparently recolonized even more slowly.

The pattern and amount of recolonization changes seasonally; one-day recolonized population densities declined from high values in Nov. to low values in Jan. and Feb. (Fig. 11.4). In Dec. the one-day recolonized population density was higher than the density of the control population and presumably it declined in a pattern similar to that of the Nov. recolonized population (Fig. 11.3). By comparison, densities of recolonized populations after one day in Jan. and Feb. were less than half that of their respective control populations and subsequently increased to the mean control population density after 28 days in Feb. and to almost four times the mean control density after 27 days in Mar. In Apr. the recolonized population density after 32 days was more than twice the control density but in May the density of recolonists after 39 days was only 1.3 times that of the control population.

The instar composition of all one-day recolonist populations differed significantly (χ^2 tests, Appendix 7.2) from their respective control populations and from each other. The dramatically large recolonist populations after one day in Nov. and Dec. contained a high proportion (59 - 75%, Table 11.2) of

Table 11.1 Structure (percent composition) of control and recolonization populations of *Cycloleberis*. No instar VII males found. ( ) = gravid females as percent of total population.

Time (days)	Instar I	II	III	IV ♂	IV ♀	V ♂	V ♀	VI ♂	VI ♀	VII ♀	VII ♀
0 control n = 138	3.6	0	0	2.9	9.4	11.6	7.3	15.2	15.2	34.8	(31.8)
1 n = 208	75.0	1.4	4.8	3.4	3.4	4.3	1.4	4.3	1.0	1.0	(0)
4 n = 178	28.1	0	5.6	6.7	13.5	13.5	16.9	9.0	3.9	2.8	(1.7)
8 n = 186	21.5	4.8	4.8	7.5	10.2	15.1	25.3	6.5	2.7	1.6	(0)
16 n = 182	5.5	5.0	0	9.3	9.3	23.1	16.5	16.5	9.3	5.5	(2.8)
26 n = 211	13.3	4.3	3.3	11.4	10.0	18.0	17.5	10.9	6.6	4.7	(2.4)
26 control n = 183	7.1	3.8	1.1	2.7	5.5	14.8	14.8	14.2	14.2	21.9	(19.1)

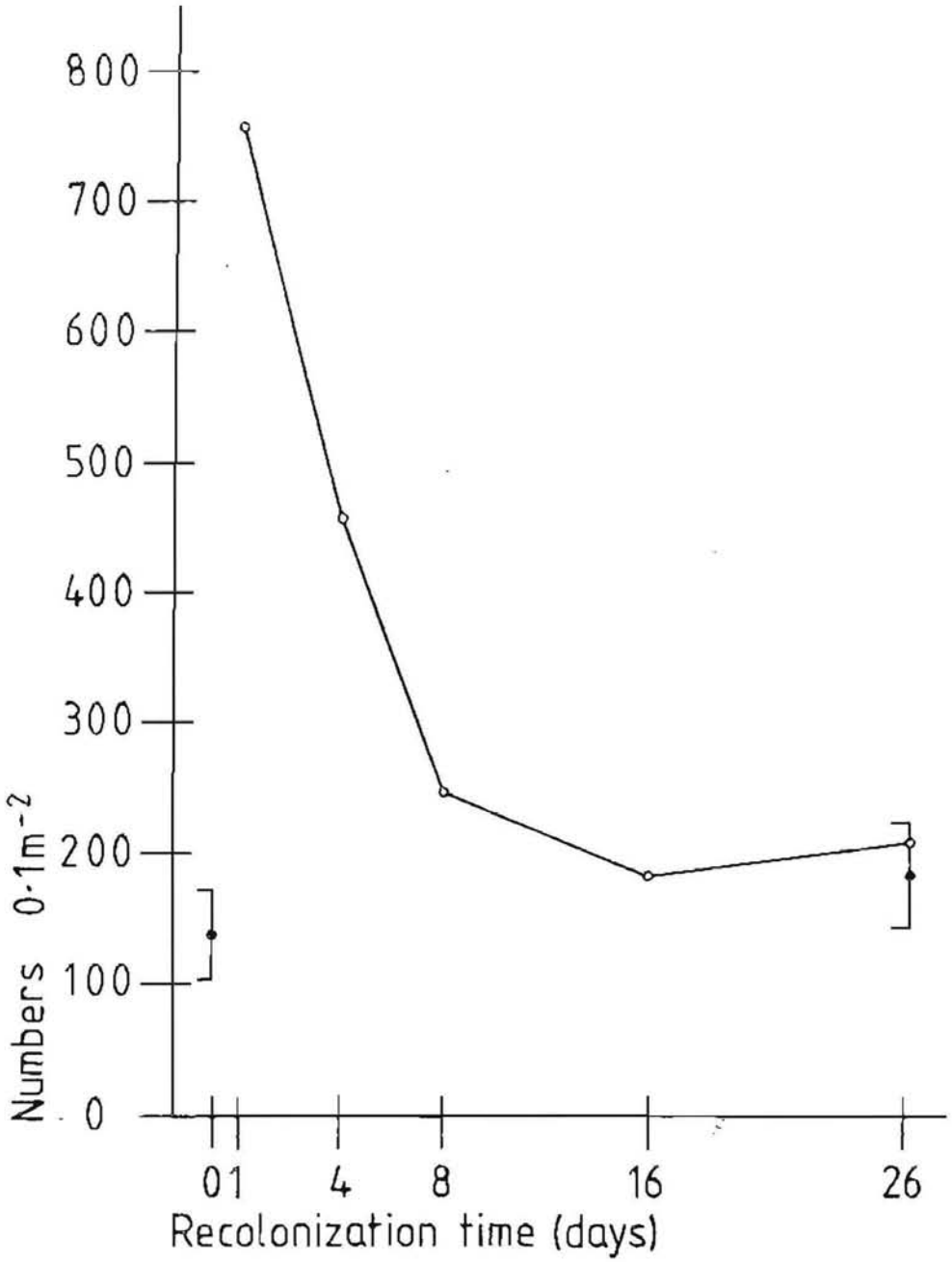

Fig. 11.3 Changes in the density of recolonized *Cycloleberis* (open circles) with time compared with control mean densities (closed circles) (± 95% confidence limits).

Table 11.2 Percent composition of control and recolonized populations of *Cyclocleberis*, Nov. 1979 - May 1980. No instar VII males found. C, control; D, days available for recolonization.

		Instar									
	n	I	II	III	IV		V		VI		VII
					♂	♀	♂	♀	♂	♀	♀
9 Nov. C	138	3.6	0	0	2.9	9.4	11.6	7.3	15.2	15.2	34.8
10 Nov. 1D	208	75.0	1.4	4.8	3.4	3.4	4.3	1.4	4.3	1.0	1.0
6 Dec. C	183	7.1	3.8	1.1	2.7	5.5	14.8	14.8	14.2	14.2	21.9
6 Dec. 1D	220	59.1	20.0	0.5	0.9	2.3	5.0	5.5	2.7	3.6	0.5
6 Dec. 26D	211	13.3	4.3	3.3	11.4	10.0	18.0	17.5	10.9	6.6	4.7
23 Jan. C	145	4.1	3.5	4.8	0.7	0	6.2	6.9	20.7	18.6	32.4
23 Jan. 1D	20	20.0	20.0	15.0	0	0	5.0	20.0	0	15.0	5.0
20 Feb. C	153	23.5	16.3	13.7	0.7	0.7	10.5	5.2	11.1	13.7	4.6
20 Feb. 1D	20	20.0	35.0	35.0	0	5.0	0	0	0	5.0	0
20 Feb. 28D	71	33.8	11.3	15.5	0	0	11.3	2.8	1.4	19.7	2.8
19 Mar. C	59	0	3.4	10.2	1.7	6.8	15.3	3.4	3.4	35.6	17.0
19 Mar. 27D	120	0.8	11.7	9.2	3.3	5.8	9.2	9.2	5.8	40.8	4.2
20 Apr. C	92	0	1.1	10.9	4.4	8.7	5.4	7.6	18.5	20.7	22.8
20 Apr. 32D	140	0	0.7	6.4	10.0	10.0	6.4	10.7	10.7	26.4	13.6
29 May C	121	0	1.7	8.3	6.6	9.9	8.3	3.3	19.0	19.0	22.3
29 May 39D	77	0	0	7.8	13.0	18.2	2.6	6.5	9.1	10.4	23.4

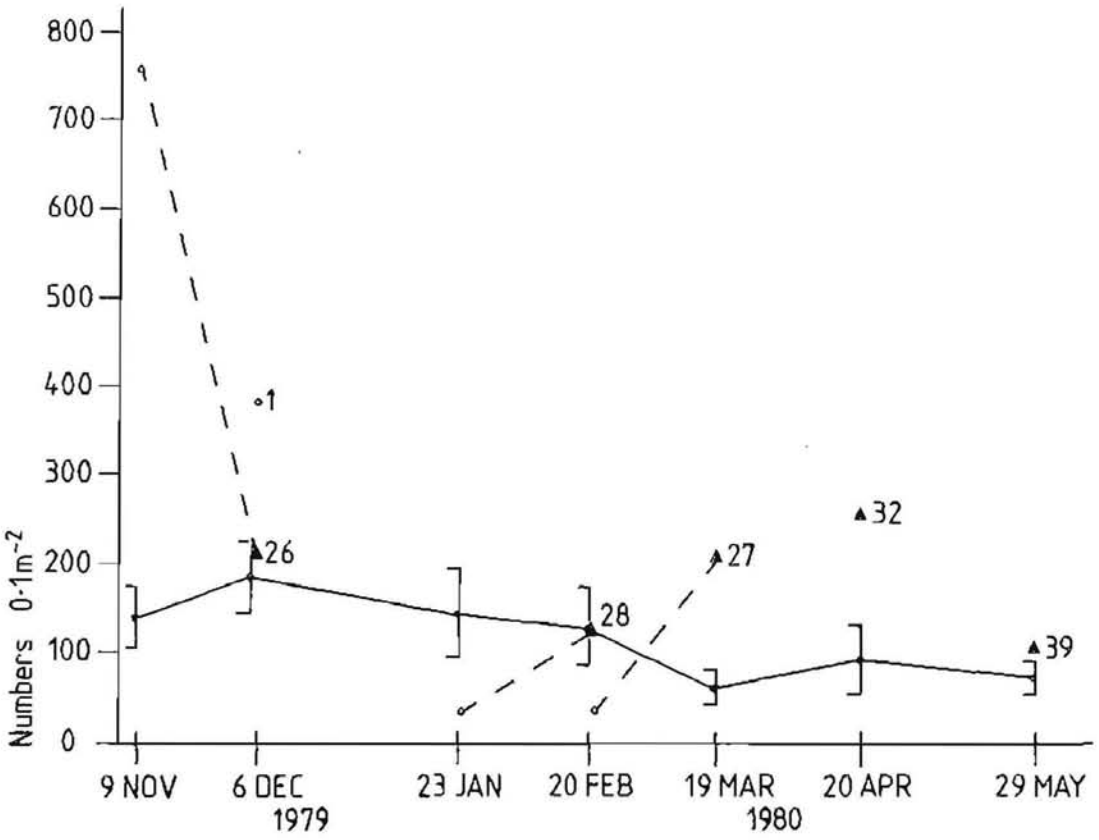

Fig. 11.4 Seasonal differences in densities of *Cycloleberis* in control population (closed circles) (mean ± 95% confidence limits) and after 1 (open circles) and 26 - 39 (triangles) days recolonization.

first instar individuals and instars I - III composed the majority (55 - 90%) of one day recolonists in the other two months. It is notable that although these instars were far more abundant (21 - 36 0.1 m^{-2}, Fig. 4.4) in Feb. than in Nov. - Dec., the Feb. one-day recolonization was low (Fig. 11.4). Thus first instar individuals were the principal short-term recolonists but the intensity of recolonization was not related to their density in the control population. Instars II and III were the next most abundant one-day recolonists and recolonization by other instars was slow.

The structures of all one month (26 - 39 days) recolonized populations differed significantly from their initial and final control population structures and from each other (χ^2 tests, Appendix 7.2). There was no obvious pattern to differences between recolonized and control populations indicating that the bucket sand habitat did not favour any particular instar or sex. Instead the 26 - 39 day duration of these experiments may be too brief and the habitat area available for recolonization too small for the recolonist population to attain a steady equilibrium.

HIPPOMEDON WHERO

Recolonization occurred throughout the 26 days of this experiment (Fig. 11.5) although the recolonized density at day four was lower than at day one. After one day the recolonized population density approached the control population density and exceeded it after about eight days. By day 26 the recolonized population density was almost twice that of the control population. There were significant changes in the structures of the various populations (Table 11.3, Appendix 7.3) and the composition of the control population changed significantly during the experiment. Although the day one recolonized population composition differed significantly from the initial control, the day four population did not differ significantly from either the initial control nor the day one population. During the remainder of the experiment the successive recolonized populations continued to differ significantly from each other and from both controls. The day 26 recolonized population did not however, differ significantly in composition from the final control, indicating that although its density was high, its composition was at equilibrium with the in situ (control) population. Despite these significant differences in population compositions, there is no clear indication that juveniles, males or females were proportionately more important recolonists at any stage and gravid females appeared to colonize the defaunated sand as readily as non-gravid females (Table 11.3).

The mean size of juveniles in all recolonized populations was significantly larger ($p < .001$ - $< .01$, t-tests, Appendix 7.4) than in the initial control. During the experiment the mean juvenile size for the control population increased so that although the mean size of the initial (1 - 16 day) juvenile recolonists did not differ significantly from the final (26 day) control population, day 26 colonist juveniles were significantly larger.

Table 11.3 Structure of control and recolonized (0 - 26 days) populations of *Hippomedon* during Nov. - Dec. 1979. ( ) = gravid females as percent of total population.

Time (days)	Juveniles			Males			Females		
	frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD
0 control n = 152	59.9	.229	.018	23.0	.388	.028	17.1 (11.2)	.422	.043
1 n = 108	50	.244	.026	29.6	.385	.033	20.4 (13.0)	.422	.047
4 n = 87	56.3	.241	.026	26.4	.378	.035	17.3 (12.6)	.433	.032
8 n = 95	63.2	.242	.025	32.6	.392	.028	4.2 (2.1)	.419	.063
16 n = 116	52.6	.239	.024	31.9	.391	.031	15.5 (12.1)	.438	.040
26 n = 125	70.4	.249	.028	26.4	.392	.028	3.2 (3.2)	.425	.035
26 control n = 247	68.0	.237	.020	25.5	.369	.040	6.5 (5.2)	.430	.061

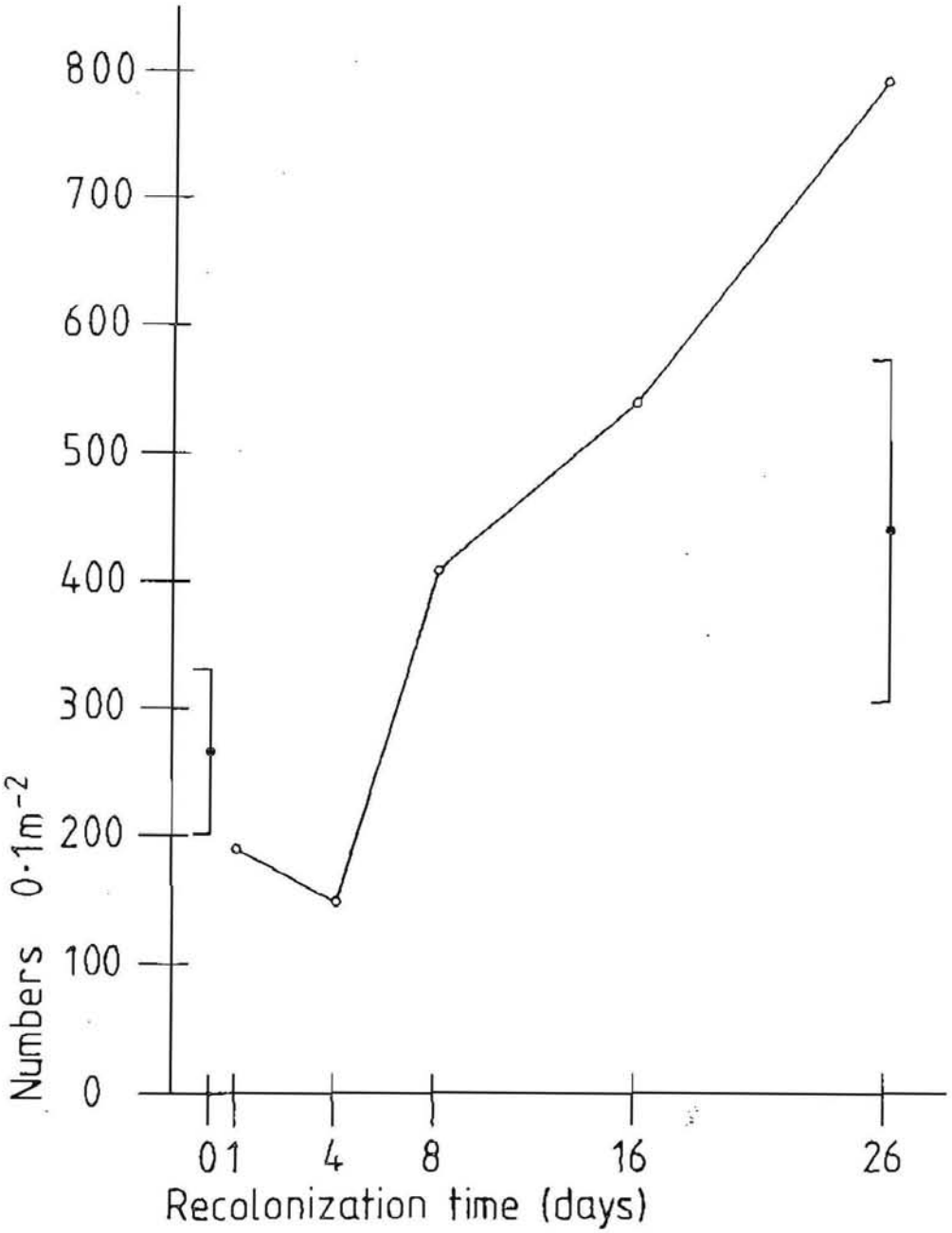

Fig. 11.5 Changes in the density of recolonized *Hippomedon* (open circles) with time compared with control mean densities (closed circles) (± 95% confidence limits).

The mean size of males in the control population decreased significantly during the experiment (Appendix 7.4) but, with the exception of the eight-day recolonists, the mean sizes of males recolonized were not significantly different from males of the initial control populations. Further, with the exception of the day four males, recolonist males were significantly larger than males of the final control population. Thus it seems that the larger males recolonized more readily than smaller males. Females of all sizes apparently recolonized equally since there were no significant differences between the mean female sizes of either control and any of the recolonized populations (Appendix 7.4). Indeed, even gravid females were equally abundant in recolonist populations and in control populations (Table 11.3).

As in *Cycloleberis*, the amount and pattern of recolonization by *Hippomedon* changes seasonally. Recolonized population density after one day was 70% of the control density in Nov. but this declined steadily through Dec. (59.5%) and Jan. (36%) to about 10% in Feb. (Fig. 11.6). The changes in monthly recolonist densities relative to control densities are less regular however, with the Dec. 26-day density almost double the control density but those for Feb. - May all being less than their controls. Indeed, densities of 27 - 39 day recolonist populations for the period Feb. - May are all close to 100 individuals 0.1 m^{-2} implying that these populations have reached a stable maximum carrying capacity which is lower than the control habitat carrying capacity and to some extent more stable than the control habitat.

The composition of all one-day recolonist populations differed significantly (χ^2 tests, Appendix 7.2) from their control populations except during Jan. In most cases the recolonist populations contained a lower proportion of juveniles, a higher proportion of males and of females (Table 11.4). Recolonist juveniles were significantly larger (t-tests, Appendix 7.5) than control population juveniles for Nov. and Dec. but differences were not significant in Jan. and Feb. There were no significant differences in sizes of recolonist and control males or females except in one month.

Structures of the longer-term recolonist populations differed significantly (Appendix 7.2) from their initial and their final control population compositions, and from each other except for the Mar. 27-day and the Apr. 32-day populations. The proportion of females was similar in each recolonist population and its respective final control population (Table 11.4), but the proportions of juveniles

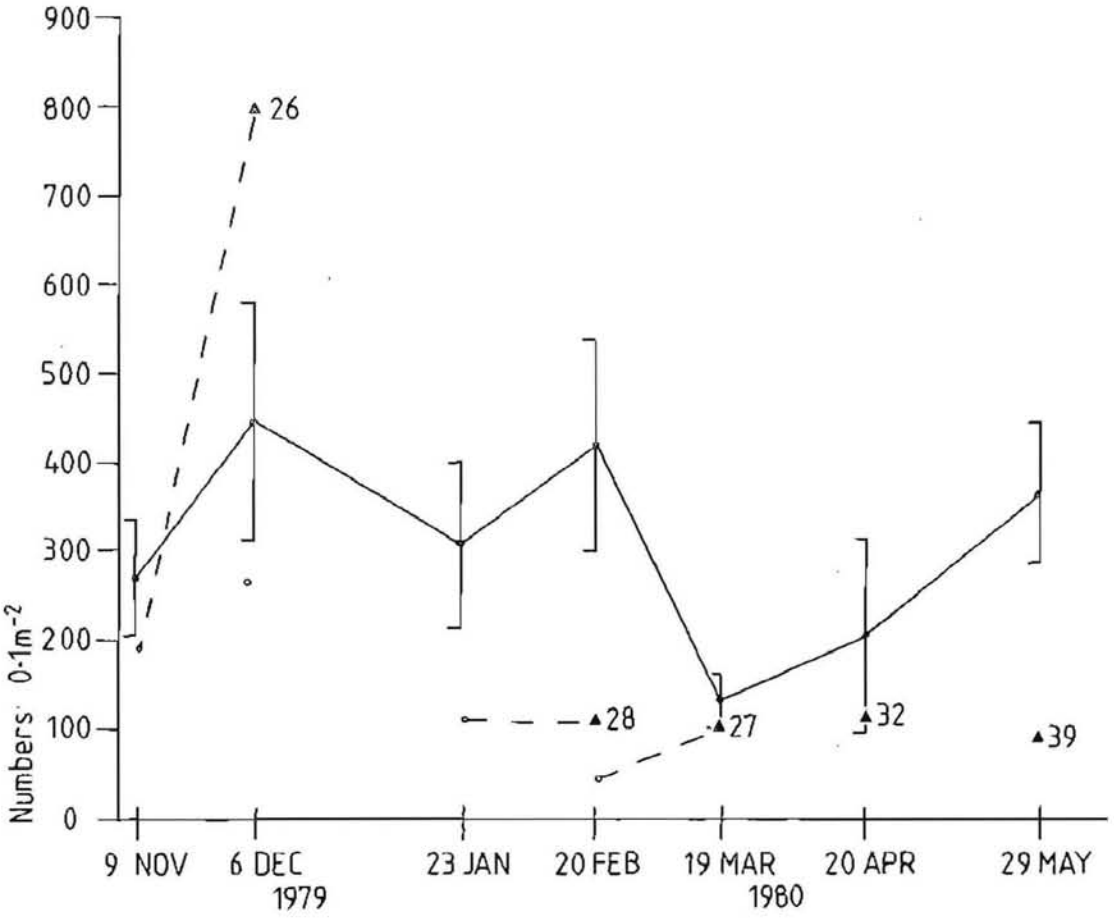

Fig. 11.6 Seasonal differences in densities of *Hippomedon* in control population (closed circles) (mean ± 95% confidence limits) and after 1 (open circles) and 26 - 39 (triangles) days recolonization.

Table 11.4 Seasonal changes in the structure of control and recolonized populations of *Hippomedon*.

Time (days)	n	Juveniles			Males			Females		
		frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD
9 Nov. C	152	59.9	.229	.018	23.0	.388	.028	17.1	.422	.043
10 Nov. 1D	108	50.0	.244	.026	29.6	.385	.033	20.4	.422	.047
6 Dec. C	247	68.0	.237	.020	25.5	.369	.040	6.5	.430	.061
6 Dec. 1D	100	64.0	.249	.027	20.0	.394	.036	16.0	.455	.038
6 Dec. 26D	125	70.4	.249	.028	26.4	.392	.028	3.2	.425	.035
23 Jan. C	215	32.1	.261	.034	52.1	.349	.040	15.8	.393	.056
23 Jan. 1D	63	28.6	.269	.030	55.6	.349	.044	15.9	.365	.054
20 Feb. C	207	41.6	.254	.032	41.0	.343	.032	17.4	.356	.037
20 Feb. 1D	25	40.0	.250	.035	48.0	.356	.048	12.0	.373	.025
20 Feb. 28D	63	25.4	.254	.039	60.3	.355	.032	14.3	.361	.045
19 Mar. C	130	14.6	.258	.030	44.6	.348	.034	40.8	.366	.044
19 Mar. 27D	59	25.4	.272	.028	35.6	.344	.028	39.0	.363	.044
20 Apr. 32D	66	28.8			34.8			36.4		
29 May 39D	53	7.6			35.8			56.6		

and males varied between pairs of populations, apparently at random. Thus although recolonized populations appeared to attain a density equilibrium after less than 27 days, their composition was quite variable and not at equilibrium with the control populations.

Only in Dec. were there any significant differences in mean sizes of juveniles and of males between recolonized and control populations (Appendix 7.5). In both cases the mean sizes of the recolonists were significantly larger than in the control populations (Table 11.4).

PATUKI ROPERI

Initial recolonization by *Patuki* was slow (Fig. 11.7) but became more rapid after the fourth day. The recolonist population attained peak density (210 0.1 m^{-2}) by day 16 but this was only 60% of the control population density. Thereafter the density of recolonists declined to less than half of the control density by day 26.

During the experiment there was no significant change in structure of the control population (χ^2 tests, Appendix 7.6) but the compositions of all recolonist populations were significantly different from both controls. Further, they differed significantly from each other except for the final pair, 16 and 26 days. This indicates that the recolonist population failed to reach an equilibrium with the control population but that after 16 days it was approaching an equilibrium of its own. While the early recolonists were dominated by juveniles and males (Table 11.5), females composed the largest portion and juveniles the smallest portion of the recolonist population near equilibrium, quite opposite to their order of abundance in control populations.

Data on sizes of control and recolonist juveniles, males and females are few and tests inconclusive (Appendix 7.7). They indicate however, that the recolonist population at equilibrium may consist of smaller males and females than the control population.

One-day recolonization varied seasonally (Fig. 11.8) but this seemed unrelated to other factors. Numbers of recolonists were low, except during Dec., precluding reliable analysis of differences in population structures and mean sizes of each sex.

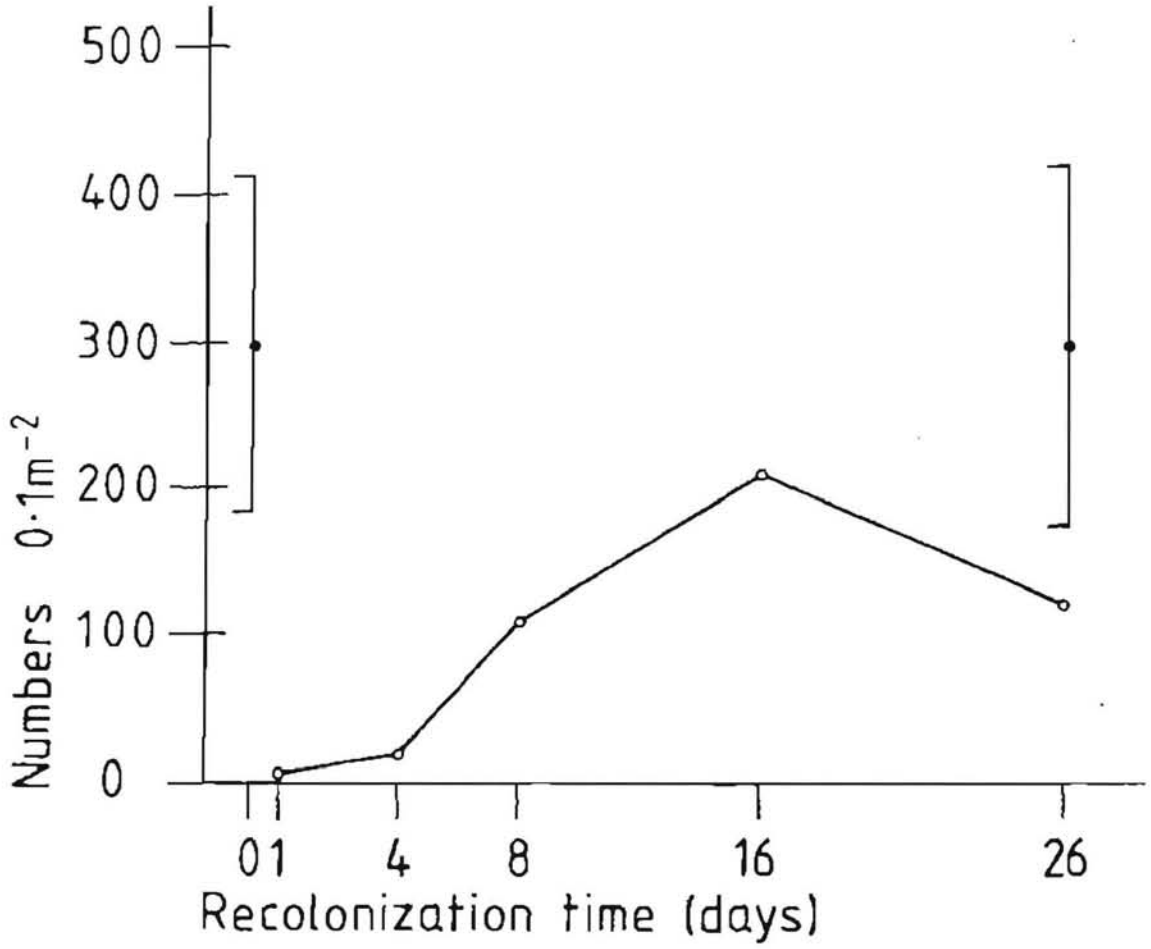

Fig. 11.7 Changes in the density of recolonized *Patuki* (open circles) with time compared with control mean densities (closed circles) (± 95% confidence limits).

Table 11.5 Structure of control and recolonized populations of *Patuki* during Nov. - Dec. 1979.

Time (days)	Juveniles			Males			Females		
	frequency %	size $\bar{x}$	SD	frequency %	size $\bar{x}$	SD	frequency %	size $\bar{x}$	SD
0 (undisturbed)	62.4	.420	.074	18.2	.627	.076	19.4	.917	.145
n = 170									
1	66.7	.563	.124	33.3	.625	-	0	-	-
n = 3									
4	60.0	.588	.065	30.0	.558	.038	10.0	.975	-
n = 10									
8	65.1	.411	.059	11.1	.543	.028	23.8	.708	.058
n = 63									
16	23.4	.432	.073	33.9	.614	.075	42.7	.862	.148
n = 124									
26	27.5	.426	.106	27.5	.632	.067	45.0	.892	.119
n = 69									
26 (undisturbed)	64.9	.442	.073	21.0	.617	.065	14.1	.952	.150
n = 262									

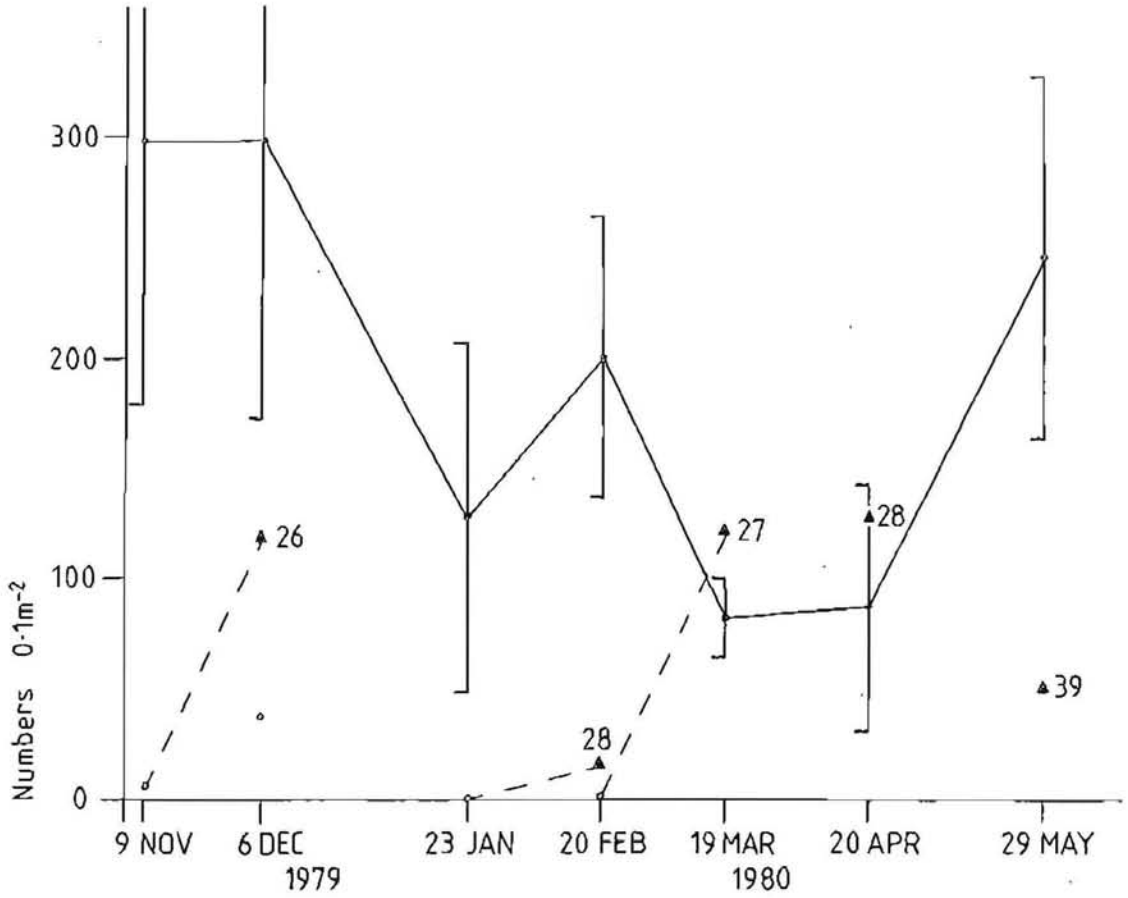

Fig. 11.8 Seasonal differences in densities of *Patuki* in control population (closed circles) (mean ± 95% confidence limits) and after 1 (open circles) and 26 - 39 (triangles) days recolonization.

A remarkable feature of the 26 - 39 day recolonist populations is that three of the five populations attained densities of 120 - 130 0.1 m^{-2} (Fig. 11.8), possibly an equilibrium density which was largely independent of factors affecting the control population density. Other unaccounted factors or simply experimental errors may have caused the deviations of the Feb. and May populations from the recolonist equilibrium population density.

Comparisons (Table 11.6, Appendix 7.2) show that the structure of recolonist populations differed significantly from their controls and from each other (with one exception) but no pattern was apparent. Similarly,

Table 11.6 Seasonal changes in the structure of control and recolonized populations of *Patuki*.

Time (days)	n	Juveniles			Males			Females		
		frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD
9 Nov. C	170	62.4	.420	.074	18.2	.627	.076	19.4	.917	.145
10 Nov. 1D	3	66.7	.563	.124	33.3	.625	-	0	-	-
6 Dec. C	262	64.9	.442	.073	21.0	.617	.065	14.1	.952	.150
6 Dec. 1D	22	36.4	.391	.030	22.7	.680	.067	40.9	.847	.114
6 Dec. 26D	69	27.5	.426	.106	27.5	.632	.067	45.0	.892	.119
23 Jan. C	127	15.0	.454	.120	32.3	.673	.065	52.7	.876	.118
23 Jan. 1D	0	0	-	-	0	-	-	0	-	-
20 Feb. C	142	36.6	.464	.101	27.5	.609	.109	35.9	.931	.102
20 Feb. 1D	1	100.0	.375	-	0	-	-	0	-	-
20 Feb. 28D	10	60.0	.371	.029	30.0	.742	.058	10.0	.850	-
19 Mar. 1D	83	9.6	.509	.178	35.0	.670	.071	55.4	.825	.174
19 Mar. 27D	71	12.7	.539	.121	50.7	.683	.056	36.6	.929	.094
20 Apr. 32D	74	8.1			40.5			51.4		
29 May 39D	30	10.0			36.7			53.3		

there was no pattern of differences in mean sizes of juveniles, males and females between control and recolonist populations (Table 11.6, Appendix 7.5).

METAPHOXUS LITTORALIS

Very little recolonization by *Metaphoxus* occurred until after day eight and most occurred between eight and 16 days (Fig. 11.9). Further recolonization took place until day 26 when the density reached about 90 0.1 m^{-2}, only about quarter of the control population density. Although there was no significant change in the composition of the control population during the experiment (Table 11.7, Appendix 7.8), the composition of successive recolonist populations changed significantly throughout the experiment and apparently had not attained an equilibrium at day 26. There were no significant differences in composition between the day eight recolonist population and the initial control, and between the day 16 population and either control. All other recolonist populations differed significantly from both controls.

Initial recolonists were largely females (Table 11.7) but the percentage of females in recolonist populations declined with time. Juveniles were slowest to recolonize but composed 77% of the 26-day recolonist population, a markedly greater proportion than in the control population. The proportion of males in recolonist populations was relatively low. There were no overall differences in the mean sizes of juveniles, males or females in control or recolonist populations (Appendix 7.9).

One-day recolonization was extremely low during Nov. - Feb. and too few individuals recolonized for any consideration of recolonist population structure or mean size composition (Fig. 11.10). The longer-term (26 - 39 days) recolonized populations during this time attained a maximum density of 90 0.1 m^{-2} in Dec. and declined thereafter to 23 - 28 0.1 m^{-2} during Mar. to May. The constancy of density during these last three months and the nature of the short-term recolonization curve (Fig. 11.9) suggest that the recolonization habitat has a carrying capacity of less than 25% of the control habitat and that the carrying capacity was 23 - 28 0.1 m^{-2} during Mar. - May. In addition, the structures of these three recolonist populations were not significantly different from each other (Table 11.8, Appendix 7.2) but different from those of the Dec. and Feb. recolonist populations which, in turn, were significantly different. The compositions of all recolonist populations differed significantly

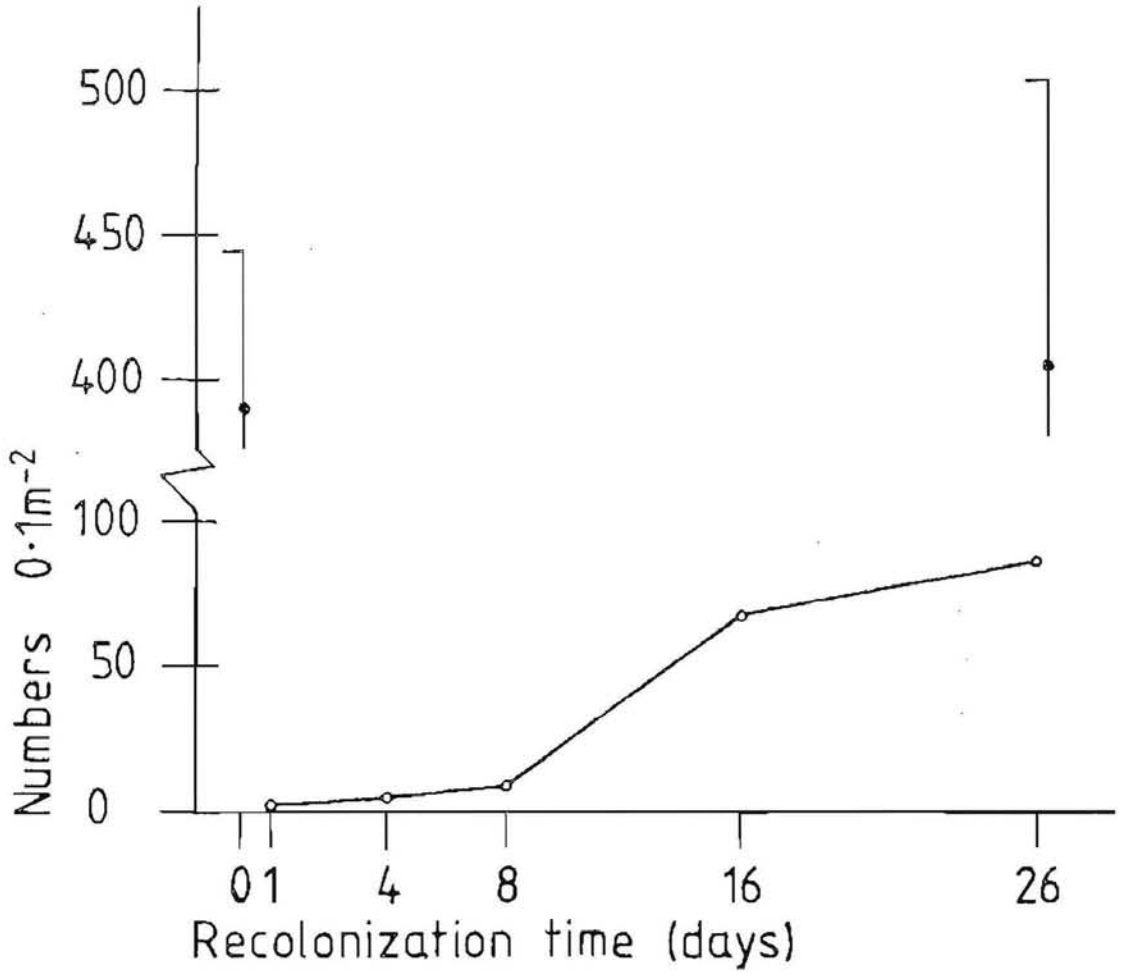

Fig. 11.9 Changes in the density of recolonized *Metaphoxus* (open circles) with time compared with control mean densities (closed circles) (± 95% confidence limits).

Table 11.7 Structure of control and recolonized populations of *Metaphoxus* during Nov. - Dec. 1979.

Time (days)	Juveniles			Males			Females		
	frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD
0 (undisturbed)	46.5	.392	.059	20.0	.590	.062	33.5	.680	.082
n = 170									
1	0	-	-	0	-	-	100.0	.750	-
n = 1									
4	0	-	-	20.0	.600	-	80.0	.594	.113
n = 5									
8	40.0	.369	.038	20.0	.550	0	40.0	.650	.108
n = 10									
16	52.5	.393	.040	20.0	.544	.058	27.5	.686	.098
n = 40									
26	77.0	.393	.045	11.5	.592	.103	11.5	.742	.085
n = 52									
26 (undisturbed)	46.3	.393	.046	25.1	.572	.070	28.6	.641	.106
n = 175									

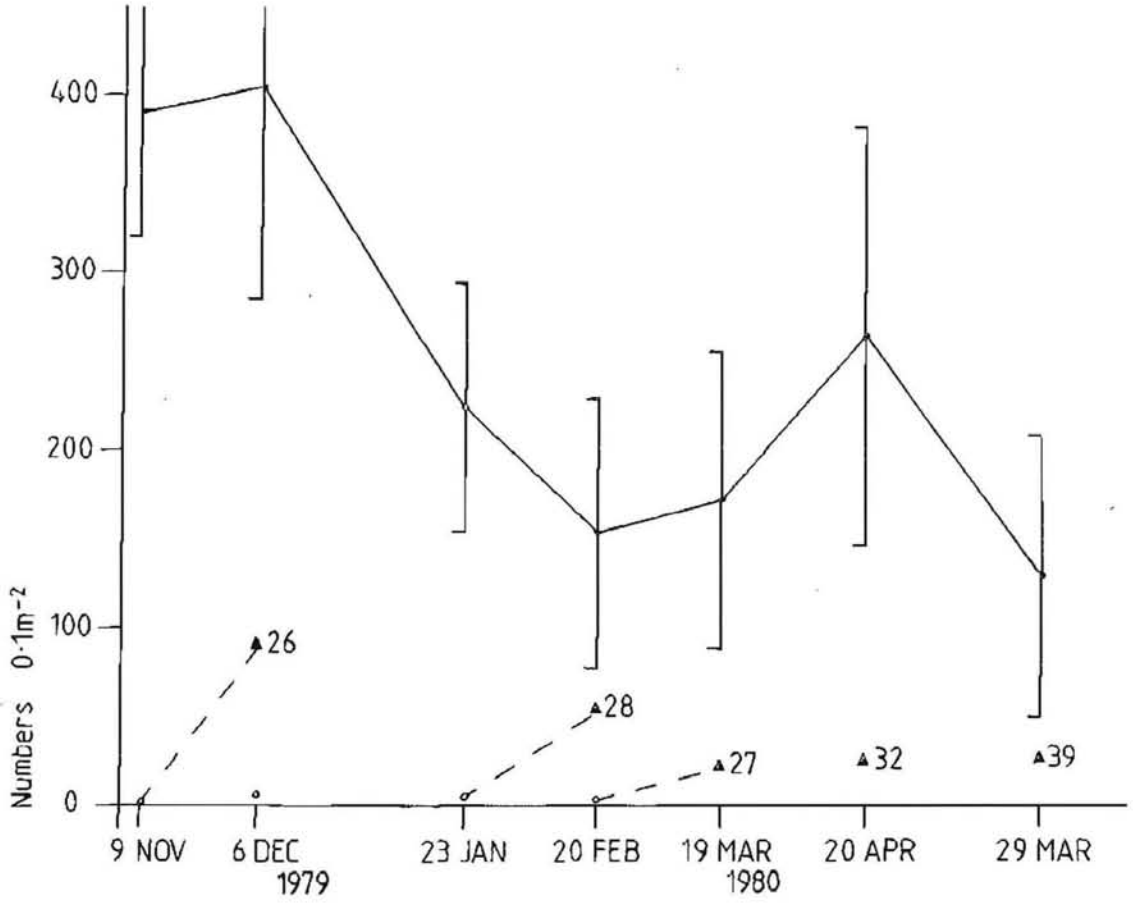

Fig. 11.10 Seasonal differences in densities of *Metaphoxus* in control population (closed circles) (mean ± 95% confidence limits) and after 1 (open circles) and 26 - 39 (triangles) days recolonization.

Table 11.8 Seasonal changes in the structure of control and recolonized populations of *Metaphoxus*.

Time	n	Juveniles			Males			Females		
		frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD
9 Nov. C	170	46.5	.392	.059	20.0	.590	.062	33.5	.680	.082
10 Nov. 1D	1	0	-	-	0	-	-	100.0	.750	-
6 Dec. C	175	46.3	.393	.046	25.1	.575	.070	28.6	.641	.106
6 Dec. 1D	3	33.3	.425	-	66.7	.525	.035	0	-	-
6 Dec. 26D	52	76.9	.393	.045	11.5	.592	.103	11.6	.742	.086
23 Jan. C	153	25.5	.412	.049	28.8	.544	.063	45.7	.599	.095
23 Jan. 1D	3	0	-	-	66.7	.550	0	33.3	.725	-
20 Feb. C	153	31.4	.390	.048	32.0	.569	.072	36.6	.586	.094
20 Feb. 1D	2	0	-	-	100.0	.525	.035	0	-	-
20 Feb. 28D	32	81.3	.381	.043	3.1	.675	-	15.6	.605	.060
19 Mar. C	171	5.3	.389	.042	39.2	.581	.064	55.5	.634	.084
19 Mar. 27D	13	61.5	.391	.057	15.4	.500	0	23.1	.542	.072
20 Apr. 32D	15	40.0			26.7			33.3		
29 May 39D	16	37.5			25.0			37.5		

from their control populations. In Dec. and Feb. juveniles were the principal recolonists and formed more than 75% of the population, but in Mar. to May juveniles, males and females were fairly equally represented (Table 11.8). There were no consistently significant differences in the mean sizes of recolonists compared with control individuals (Appendix 7.5).

PARAPHOXUS AUSTRALIS

After one day the recolonized population of *Paraphoxus* approached the control population mean density (Fig. 11.11). By the fourth day it declined to half the control density, increased to 180 0.1 m^{-2} by day eight, declined below the control mean density at day 16 and increased to twice the final control density by day 26. As expected the recolonized populations' structures differed from the initial control, from each other (with the exception of the eight-day and 16-day populations) and from the final control except the eight-day and the 26-day recolonist populations (Table 11.9, Appendix 7.10). Thus at higher densities the recolonist population structure was similar to that of the final control population.

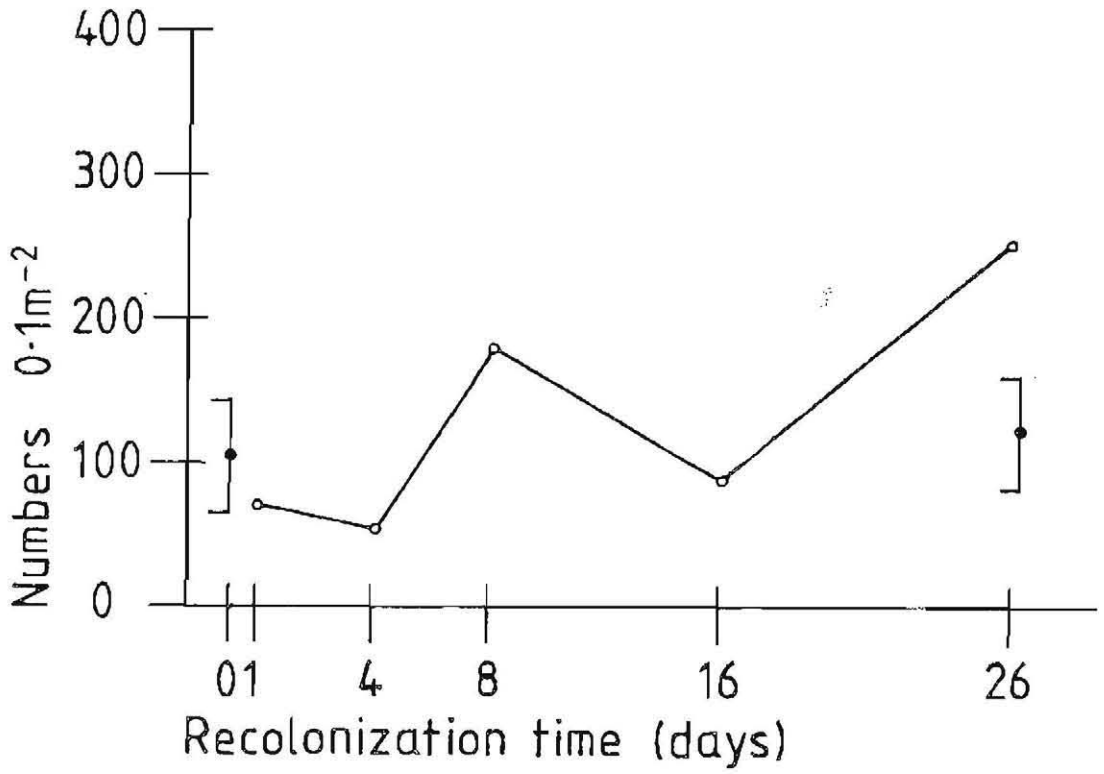

Fig. 11.11 Changes in the density of recolonized *Paraphoxus* (open circles) with time compared with control mean densities (closed circles) (± 95% confidence limits).

Table 11.9 Structure of control and recolonized populations of *Paraphoxus* during Nov. - Dec. 1979.

Time (days)	Juveniles			Males			Females		
	frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD
0 (undisturbed)	77.7	.427	.086	6.8	1.161	.080	15.5	1.289	.153
n = 103									
1	25.0	.418	.049	32.5	1.143	.097	42.5	1.166	.115
n = 40									
4	63.3	.441	.070	3.3	.925	-	33.4	1.158	.109
n = 30									
8	87.4	.426	.084	3.9	.925	.167	8.7	1.092	.178
n = 103									
16	84.9	.494	.101	3.8	1.123	.145	11.3	1.379	.320
n = 53									
26	91.0	.453	.108	2.8	.944	.157	6.2	1.058	.088
n = 144									
26 (undisturbed)	86.5	.457	.090	7.2	1.141	.356	6.3	1.168	.199
n = 111									

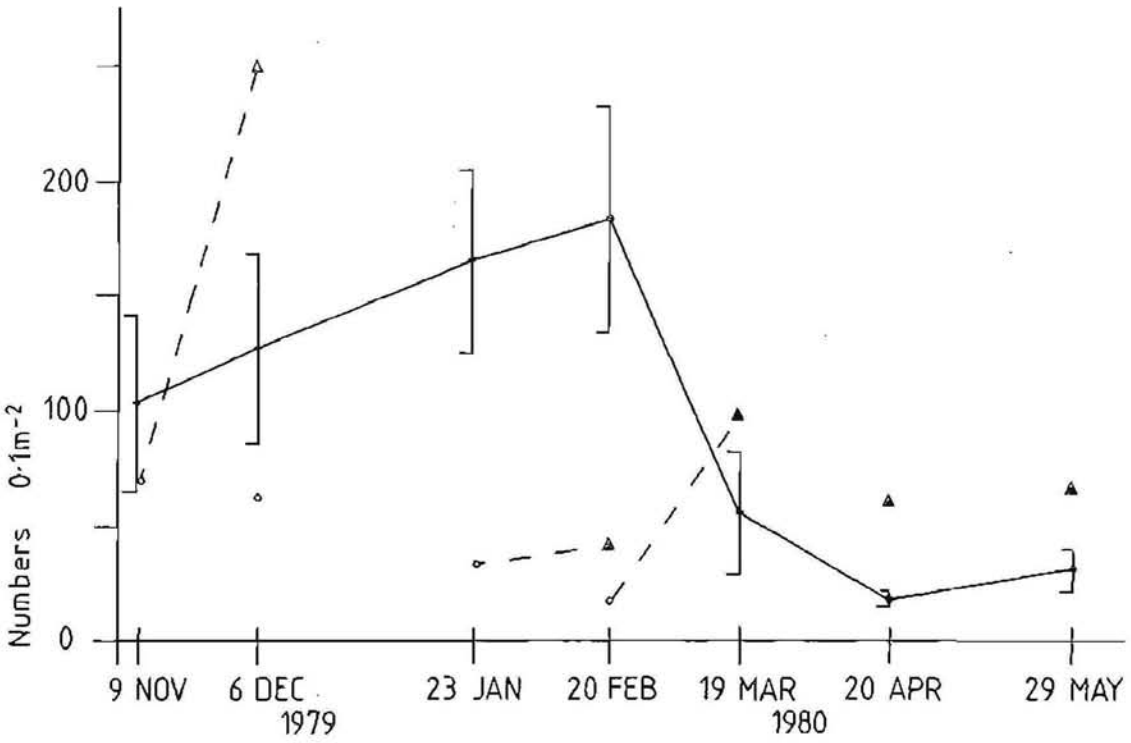

Fig. 11.12 Seasonal differences in densities of *Paraphoxus* in control population (closed circles) (mean ± 95% confidence limits) and after 1 (open circles) and 26 - 39 (triangles) days recolonization.

Table 11.10 Seasonal changes in the structure of control and recolonized populations of *Paraphoxus*.

Time	n	Juveniles			Males			Females		
		frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD	frequency %	size (h.l., m.m.) $\bar{x}$	SD
9 Nov. C	103	77.7	.427	.086	6.8	1.161	.080	15.5	1.289	.153
10 Nov. 1D	40	25.0	.418	.049	32.5	1.143	.097	42.5	1.166	.115
6 Dec. C	111	86.5	.457	.090	7.2	1.141	.356	6.3	1.168	.199
6 Dec. 1D	36	66.7	.507	.169	13.9	1.200	.074	19.4	1.204	.269
6 Dec. 26D	144	91.0	.453	.108	2.8	.944	.157	6.2	1.058	.088
23 Jan. C	165	75.8	.566	.184	4.2	1.032	.112	20.0	1.311	.310
23 Jan. 1D	19	42.1	.509	.143	5.3	.750	-	52.6	.950	.126
20 Feb. C	183	94.0	.576	.185	1.1	1.213	.053	4.9	1.156	.248
20 Feb. 1D	10	40.0	.625	.162	10.0	.925	-	50.0	.950	.108
20 Feb. 28D	24	54.2	.648	.166	4.2	.900	-	41.6	1.050	.238
19 Mar. C	54	64.8	.810	.136	5.6	1.150	.156	29.6	1.090	.227
19 Mar. 27D	57	31.6	.714	.118	3.5	1.400	.636	64.9	1.240	.425
20 Apr. C	18	50.0			0			50.0		
20 Apr. 32D	35	60.0			8.6			31.4		
29 May C	31	61.3			3.2			35.5		
29 May 39D	39	23.1			25.6			51.3		

At day one females and males were the principal recolonists and proportionately more abundant than in the control population. Juveniles composed over half of the recolonists by day 4 and comprised more than 85% from day 8 onwards. The proportions of males and females were less than in the control populations. There was no pattern to differences in mean sizes of juveniles and males (Table 11.9, Appendix 7.11) but recolonist females tended to be significantly smaller than females of the initial control population.

A decrease in the density of one-day recolonists occurred from Nov. to Feb. (Fig. 11.12) whereas the control population increased in density throughout this period. These changes were not accompanied by any regular changes in the compositions of either control or recolonist populations (Table 11.10), although recolonist population structures differed significantly from their controls and from each other (except Jan. and Feb.) (Appendix 7.2).

Densities of recolonist populations after 26 - 39 days also differed markedly between Nov. and May (Fig. 11.12) but there was no obvious pattern to these differences either in density or in population structure (Table 11.10, Appendix 7.2). In addition, although there were few differences between mean sizes of control and recolonist populations (Appendix 7.5), those significant differences showed that recolonists tended to be smaller than control individuals.

DISCUSSION

The rates of recolonization seen in these species are the fastest yet reported for macrofauna and similar to those reported for intertidal estuarine meiofauna (Sherman & Coull, 1980). Previous studies on macrofaunal recolonization (e.g. Boesch *et al*, 1976; Dauer & Simon, 1976; Richter & Sarnthein, 1977) however, followed recolonization over longer time periods, usually at intervals of one month and at one time only.

Sherman & Coull (1980) postulated that most of their meiofaunal recolonization was by passive transport with the tide but this seems unlikely for these Kaikoura Crustacea. All species are active burrowers, good swimmers and seem well adapted to maintain their various microhabitats under

normal sea conditions (see Chapter 10). These animals do make active forays into the plankton on some, if not most nights (Chapter 10) and, since all life history stages of all species participate in these, their principal function may be dispersal to unoccupied habitats. Certainly some activity would be required to raise individuals 350 mm above the bottom in order to enter the buckets of sand. Thus recolonization probably occurred by individuals actively leaving the bottom to swim in the water column and eventually settling in the experimental buckets of sand.

Attempts to trap emergent fauna as it left the bottom were largely unsuccessful because the inverted funnel traps used were usually knocked over by wave action. Individuals of all species were taken in these but not in sufficient numbers for any analysis.

Obviously the experimental buckets of sand presented not only uninhabited space to the colonists, but also a habitat which was in some way more attractive than the natural habitat. Indeed the extremely high density of *Cycloleberis* after one day can scarcely be attributed to colonization of unutilized space alone. Two possibilities exist: (i) treatment of the sand with hot freshwater probably lysed bacteria and microalgae on the sand grains producing a rich 'scent' which attracted the detritivorous *Cycloleberis* and possibly *Paraphoxus* also. (ii) The bucket habitat offered a hydrodynamically sheltered habitat, unusual but preferable because of its stability, because the sand particle size composition was suitable and possibly also because the bucket acted as a trap for drifting detritus. I favour the first possibility to explain most of the short-term recolonization.

Within each species certain subgroups of the population colonize 'new' habitat more readily than others, but the recolonization rate of a species may change with time independently of its abundance. For example, first instar individuals were the principal one-day recolonists of *Cycloleberis* in Nov. and Dec. but they were considerably less important in Feb. when they formed a greater proportion of the control population (Table 11.2). Further, there may be a succession in species population composition as recolonization proceeds which is independent of normal control population changes. This is seen in *Patuki* where the initial recolonist population consisting of 67% juveniles and no females changed steadily to 27.5% juveniles and 45% females after 26 days

(Table 11.5). There was no significant change in compositions of the control populations during this time.

Individual size also seems important in recolonization; recolonists of some population subgroups had a significantly larger or smaller mean size than their control populations. In *Hippomedon* for example, the mean sizes of recolonist juveniles in Nov. and Dec. were significantly larger than the mean sizes of juveniles in control populations. Recolonist females of *Paraphoxus* at the same time tended to be significantly smaller than control population females.

Different species exhibited different patterns of recolonization, probably a consequence of several factors. Important among these are the availability of recolonist individuals, species' mobilities, and the attractiveness of the new habitat. This latter factor deserves further consideration in respect of species diets. *Cycloleberis* underwent a remarkable initial recolonization, probably because the treated sand released a 'scent' which was most attractive to this detritivore. *Hippomedon* also is detrivorous but its pattern of recolonization was converse to that of *Cycloleberis*. Possibly *Hippomedon* is a slower recolonist capable of competitive displacement of the larger *Cycloleberis*. Despite its usual high mobility, recolonization by *Patuki* was slow and control population densities were approximated only after 26 days. The nature of this species mobility may provide a partial explanation: Usually it swims for short distances across the sand but rising no more than 10 - 20 mm above the sand surface. In addition, *Patuki* appears to feed on living micro-algae on sand grains and several days would be required for development of an appreciable sand-grain flora after the hot freshwater treatment. Both *Metaphoxus* and *Paraphoxus* are predators but their patterns of recolonization are quite different. *Paraphoxus* recolonized to about normal (control) density within a day and thereafter the recolonist population densities fluctuated throughout and above the range of control densities. As demonstrated by Sherman & Coull (1980) some harpacticoid copepods and nematodes, most probably detritivores, are capable of recolonization to normal densities within one tidal cycle and, given the apparent attractiveness to detritivores of the treated sand in this experiment, substantial recolonization by harpacticoids, a major food item for *Paraphoxus*, would be expected within one day. Thus the treated sand potentially offered abundant food resources for *Paraphoxus* from day one onwards. The slower recolonization by *Metaphoxus* and its failure to attain

control densities after 26 days may be attributable to a lower propensity to leave the sand and possibly to some competitive exclusion by *Paraphoxus*.

It is difficult to explain seasonal changes in the recolonization patterns of each species however, especially since initial (one day) and final (26 - 39 days) densities only were monitored. Little seasonal change in pattern is apparent in *Patuki* and *Metaphoxus*, and also in *Paraphoxus* except that there was a decrease in the amount of recolonization after Nov. - Dec. The same may be true for *Hippomedon* also but the data are inadequate. Reversal of *Cycloleberis's* Nov. - Dec. recolonization pattern occurs during Jan. - Mar. for no apparent reason. Certainly it is not simply a question of changing population structure because instars I - III, the principal recolonists for *Cycloleberis*, were more abundant in Jan. and Feb. than in Nov. and Dec. The total faunal density peaked in Dec. but one-day recolonization was greatest in Nov. and declined in Dec. Nor is any relationship with sea temperature obvious. These seasonal changes in recolonization by each species thus probably result from a complex of factors among which population structure and population density must be important.

Recolonized populations of three species appeared to reach stable equilibrium densities after 26 - 39 days between Nov. and May. For *Hippomedon* this equilibrium density was about 100 0.1 m^{-2} and generally lower than the control densities. Densities of 120 - 130 0.1 m^{-2} for recolonized *Patuki* were both lower and higher than control densities, whereas the 23 - 28 0.1 m^{-2} of recolonized *Metaphoxus* during Mar. - May was less than 25% of the control population density. The differences between these densities and their control population densities further indicate the different nature of the experimental sand habitat compared with the natural in situ sand habitat.

This study further demonstrates the dynamic, highly mobile nature of the South Bay sand crustacean assemblage showing their capabilities of maintaining preferred microhabitats within the sediment (Chapter 10) and of rapidly reoccupying parts of their habitat defaunated by storm induced catastrophic disturbances. Within the South Bay sand habitat there is a diversity of hydrodynamic situations resulting from rock outcrops, rock crevices filled with sand, etc., and the severity of storm effects on the crustaceans will vary in each situation. Thus reservoirs of each species will survive major storms and, as demonstrated here, rapidly reinvade defaunated areas, grow, reproduce and restore the total populations to more usual levels within a short time.

CHAPTER 12

LIFE-HISTORY TACTICS OF BROODING CRUSTACEANS WITH SPECIAL REFERENCE TO GAMMARIDEAN AMPHIPODS

Many of the recent publications on life-history tactics are highly theoretical and scarcely applicable to marine invertebrates because of the difficulties of obtaining reliable age-specific data on mortality and natality. Further, much of the work on marine animals has concentrated on larval development (e.g. Strathmann, 1977; Todd & Doyle, 1981) and hence is not relevant to studies of brooding Crustacea. Two recent reviews of reproductive patterns in gammaridean amphipods (Nelson, 1980; Van Dolah & Bird, 1980) provided a tangible and realistic but superficial approach by comparing a few life-history traits of species inhabiting relatively stable and unstable habitats. These publications suggest that it should be possible to predict with confidence the combinations of life-history traits of amphipods and perhaps other Crustacea inhabiting different situations.

In their analyses both Nelson (1980) and Van Dolah & Bird (1980) designated species as either epifaunal or infaunal in habitat although they realised that a diversity of microhabitats existed within each class. Basic to their discussions was the assumption that the epifaunal habitat represents a higher risk environment than the infaunal situation due to predation and environmental disturbances. While this may be true in some instances (Nelson, 1979), it is not necessarily so and there is considerable evidence indicating that predation regulates some infaunal communities (Riese, 1977; Virnstein, 1977; Hulberg & Oliver, 1980).

In habitats like the high-energy, sand bottom in South Bay, Kaikoura, there is no sessile epifauna and the few epibenthic species are highly mobile, moving continually to remain within the surface layer of shifting sediment. Very few large animals capable of capturing infaunal species within the sand were found. The only potential predators seen were three species of fish, *Pseudolabrus celidotus* and *Parapercis colias*, both epibenthic feeders known to take amphipods and other crustaceans (Graham, 1956; Russell, 1971), and the common *Tewera cranwellae*, a small benthic fish which lies in wait for prey burrowed in the sand with only its eyes exposed. Thus during normal sea

conditions the probability of capture by predators must be greatest for epifaunal dwellers and least for deep burrowing species. Major disturbances during severe storms would also affect surface dwellers and shallow burrowers more than deeper burrowing species. Consequently a combination of observations on behaviour and data on mean sediment depths inhabited (Chapter 10) provides a ranking of species mortality risks for this study. Although species sediment-depth distributions overlap considerably, *Patuki* is shallowest, *Metaphoxus* second, *Paraphoxus* third, *Hippomedon* fourth and *Cycloleberis* deepest in the sediment. Only *Patuki* can be considered epifaunal in habitat, the others are infaunal.

Perhaps the best indications of mortality risks are provided by the animals themselves in their seasonal and year to year density fluctuations. Populations subjected to high levels of density-independent mortality undergo wide fluctuations in density whereas density fluctuations are smaller in populations with low density-independent mortality (Pianka, 1970a). For invertebrates that produce several overlapping cohorts annually, the minimum mean population density expressed as a percentage of the annual maximum mean density provides a simple measure of seasonal population persistence, $P = (d_{min} \times 100)/d_{max}$ where d_{min} and d_{max} are the minimum and maximum mean densities respectively in one year. An index of the constancy of seasonal population density fluctuations between years (F) was calculated as the sum of absolute differences in P between successive years all divided by the number of comparisons (number of years minus one):

$$F = \frac{\sum |P_t - P_{t+1}|}{n-1}$$

where P_t is the seasonal persistence index for year t and n is the number of annual persistence index values compared. Populations with low mortality risks and low density-independent survival will be characterized by high persistence (P) and low fluctuation (F) values whilst the converse will typify populations exposed to high mortality risks and high density-independent mortality.

Annual minimum and maximum mean densities, and values of P and F for *Cycloleberis* and the four South Bay amphipods are given in Table 12.1. Summer maximum mean densities were quite variable between years in all except *Hippomedon*, but winter minima were less variable. Seasonal persistence (P)

Table 12.1 Maximum and minimum mean densities, persistence (P) and fluctuation (F) indicies for *Cycloleberis*, *Hippomedon*, *Patuki*, *Metaphoxus* and *Paraphoxus* at South Bay, Kaikoura, Oct. 1978 - Sept. 1979, Oct. 1979 - Oct. 1980.

	Density (nos 0.1 m^{-2})						
	maximum		minimum		P		F
	1978 - 79	1979 - 80	1978 - 79	1979 - 80	1978 - 79	1979 - 80	
Cycloleberis	349.3	185.1	30.0	19.0	8.6	10.3	1.7
Hippomedon	507.2	543.0	120.0	130.0	23.7	23.9	0.2
Patuki	580.8	299.4	30.0	78.0	5.2	26.1	20.9
Metaphoxus	168.0	405.7	41.3	38.0	24.6	9.4	15.2
Paraphoxus	438.4	183.0	12.0	18.0	2.7	9.8	7.1

differed markedly between years in *Patuki* and in *Metaphoxus* but it was almost constant in *Hippomedon* and *Cycloleberis*. Species ranking in order of decreasing fluctuation (F) is the same as their ranking in order of increasing sediment depth inhabited (Chapter 10) (except that *Hippomedon* has a slightly lower index value than *Cycloleberis*) and hence in order of decreasing mortality risk. Do the combinations of life-history traits in each of these species show a similar gradation indicative of their population mortality risks and stability?

The principal reproductive traits of each species are summarized in Table 12.2. In the initial consideration of these data it is simplest to disregard *Cycloleberis* because, being an ostracod, its life history has evolved with phylogenetic constraints (see below) different from those of the four amphipods. Within the Table species are arranged in order of increasing mortality risk from left to right.

Few trends in the life-history traits of the amphipods are apparent across the Table. With increasing mortality risk the following occurs; (a) populations consist of more simultaneous cohorts, (b) more cohorts are produced annually, and (c) maximum female longevity tends to decrease. It is notable that no clear relationship exists between mortality risk and (a) female age at maturity, (b) female size at maturity, (c) number of broods per female, (d) absolute brood size or brood size per standard (6 mm long) female, (e) egg size, and (f), brood mortality. The reduction in female maximum longevity reflects the increasing mortality risks due to predation and physical disturbance inherent in dwelling near the sand surface. Surprisingly there is no correlated reduction in female size at maturity. Instead, life history adaptation to increased mortality risk among these amphipods entails increasing the size/age diversity of the population to minimize the effects of size/age specific mortality. This has occurred by reducing female maximum longevity and shortening the interval between production of successive cohorts so that more cohorts are produced annually and remain in the population relatively longer.

Recently two independent collocations of amphipod life-history tactics arrived at some common and interesting conclusions. Nelson (1980) found that females of epifaunal species matured at larger mean sizes and produced more eggs per brood than infaunal species. Van Dolah & Bird (1980) confirmed

Table 12.2 Summary of the major life history traits of the five Kaikoura Crustacea (S, summer; W, winter; brackets indicate that an event event may be repeated once more in some years; *, standardized brood size calculated from regression analysis of female size and brood size).

	Cyclocleberis	*Hippomedon*	*Paraphoxus*	*Metaphoxus*	*Patuki*
No. simultaneous cohorts	3	4 (5)	5-9	6-7	7-10
No. cohorts/year	1 (2)	5	7-8	10-11	11-12
Maximum ♀ longevity (days) S	2.3-3.3y	214-244	220-293	191-205	147-177
W		260-363	373-383	214-243	195-271
Estimated no. instars	7	11	19	9	16
Instar no. at maturity	7	4	7	4	5
Age at maturity as % max. longevity S	78-85	37	75-88	45-55	38-46
W		43-50	51-63	42-60	58-61
♀ size at maturity (total length, mm)	5.682	3.8	6.6	3.1	6.8
Max. no. broods/♀	1	8	13	7	12
$\bar{x}$ brood size	37.04, 1-47	3.356, 1-8	19.286, 1-40	2.705, 1-9	6.673, 1-24
Total eggs/♀ lifetime	37.04	10.068	77.144	8.115	20.019
Brood mortality %	0	14.2	34.5	30.4	0
Recruitment periods/year	1 (2)	1 (2)	1 (2)	1 (2)	1 (2)
Time of major recruitment	Dec.-Feb.	Sept.-Mar.	Oct.-Dec./Feb.	Oct.-Dec.	Nov.-Dec.
>50% ♀s gravid	Aug.-Dec., 5	Sept.-Mar., 7	Sept.-Mar., 7	Aug.-Nov., 4	Aug.-Mar., 8
$\bar{x}$ egg length (mm)	0.773	0.434	0.508	0.375	0.532
Brood size of 6 mm ♀*	40.099	4.747	14.492	6.395	0.948
Relative egg size (egg length/♀ size at maturity	.136	.096	.077	.121	.078
Survival pattern	C	A	B	A	B

this relationship of more eggs per brood in epifaunal versus infaunal species. They also reported that mean egg size was larger in infaunal species compared with epifaunal species and postulated that adult mortality risk was correlated positively with brood size and negatively with egg size. This hypothesis assumes that the epifaunal habitat has a higher mortality risk than the infaunal habitat, an assumption which, as discussed above, probably is true in many situations but remains questionable in others.

Data obtained in the present study contradict these findings and Van Dolah & Bird's (1980) hypothesis. *Patuki*, the only truly epifaunal species among the South Bay amphipods, matures at a large size (females) but produces very small broods of large eggs. At the other extreme, *Hippomedon* matures at a small size and produces few eggs per brood, but the eggs are not large, especially when compared with those of *Patuki*. Further, neither *Metaphoxus* nor *Paraphoxus* show the predicted correlations between mortality risks and brood size or egg size.

I see three possible reasons for the failure of this hypothesis: 1. Nelson (1980) and Van Dolah & Bird (1980) apparently knew little of the true habitats of the species examined and seem to have misclassified many epifaunal species as infaunal and vice versa. Typically, most oedicerotids are epifaunal as described for *Patuki* (Chapter 10) and personal observations have shown that *Amphiporeia virginiana* behaves similarly. Species of *Ampelisca*, especially *A. abdita* and *A. vadorum*, are epifaunal because they usually sit in the tops of their tubes raised above the sediment surface (Mills, 1967). Perhaps species found living under stones are more properly infaunal in very coarse sediment, particularly when they are compared with species living freely in pools, on rock and among algae. If so, then *Gammarus duebeni*, *G. setosus*, *G. obtusatus*, *G. finmarchicus* (Steele & Steele, 1969, 1970a,b, 1975a) and *G. oceanicus* (Steele, 1976) should be considered infaunal. 2. Both Nelson's (1980) and Van Dolah & Bird's (1980) epifaunal species are overwhelmingly dominated by species of *Gammarus* and other members of the Gammaridae, a family notable for its primitive features (Barnard, 1974) including the production of large numbers of eggs per brood. 3. All three traits considered here are inter-related (see below) and vary independently only within moderate limits.

A further very recent review (Wildish, 1982) adds little or nothing to the study of amphipod life history tactics.

Age-specific mortality, specifically the relative intensities of pre-reproductive and adult mortalities, is central to the bet-hedging theory of life-history tactics and some measure of these for the Kaikoura crustaceans is necessary to test its predictions. Where individuals cannot be aged reliably and in populations where changes in composition cannot be followed because successive cohorts overlap, female size-frequency data for a period of one year provide an indication of size-specific, and hence age-specific survival and of the annual population mortality pattern.

Female survival better illustrates the effects of mortality on the reproductive potential of each species. Each line shows female survival after adjusting frequencies of embryos and juveniles by the population sex ratio at recruitment (1:1 in all species, see Chapters 5 - 8). It should be noted that such plots (Fig. 12.1A - D) contain data for several cohorts and that while size (x-axis) is related to age, this relationship may be neither linear nor constant throughout its range. The value of such plots lies in providing comparative patterns of mean survival and mortality. Further, in the absence of better data, they can be used to provide crude estimates of instar-specific survivorships, net reproductive rates (R_0) and intrinsic rates of natural increase (r).

Annual size-specific survival curves for the four amphipods (Figs 12.1 A - D) show no obvious relationship with habitat mortality risk. Curves for all species show (a) high juvenile mortality at and following recruitment, (b) a period of high survival from about the size of male maturity to after female maturity, followed by (c) a decline to low numbers at larger size. Note that points forming phase (b) of the curve do not necessarily form a straight, horizontal or declining line and in *Hippomedon*, *Metaphoxus* and *Paraphoxus* they rise indicating increased frequencies in larger size classes resulting from slower growth rates at these sizes.

Two patterns of size-specific survival are apparent: A, in *Hippomedon* and *Metaphoxus* 20 - 33% of female embryos survive recruitment, growth rates slow markedly after about the size of male maturity, and mortality is low until after female maturity when it increases sharply. In contrast (pattern B), *Paraphoxus* and *Patuki* suffer drastic mortality (89 - 94% mortality or 6 - 11% survival) at recruitment, post-recruitment growth rates seem little changed, mortality is more or less constant but moderate from before female maturity,

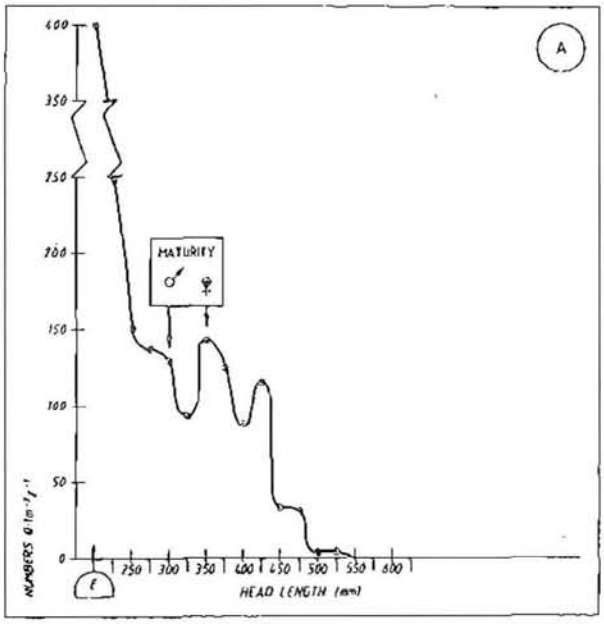

Fig. 12.1A Size-specific survival of female *Hippomedon*, Oct. 1978 - Oct. 1979 (numbers 0.1 $m^{-2}y^{-1}$). Densities of embryos (E) and juveniles corrected for sex ratio of 1:1.

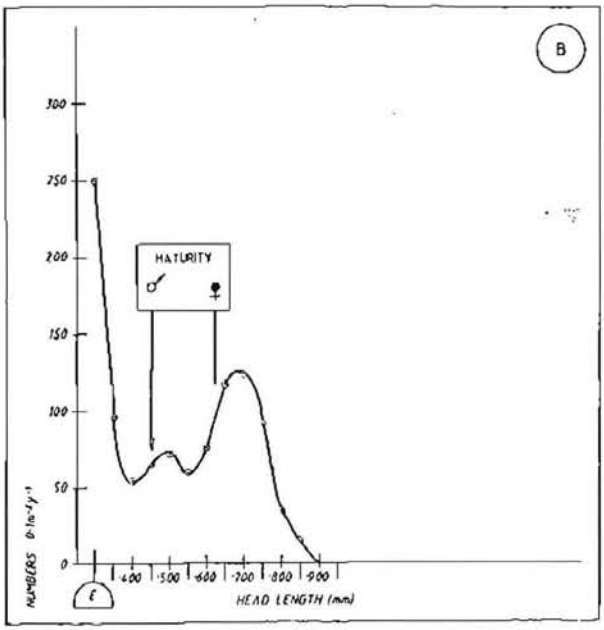

Fig. 12.1B Size-specific survival of female *Metaphoxus*, Sept. 1978 - Sept. 1979 (numbers 0.1 $m^{-2}y^{-1}$). Densities of embryos (E) and juveniles corrected for sex ratio of 1:1.

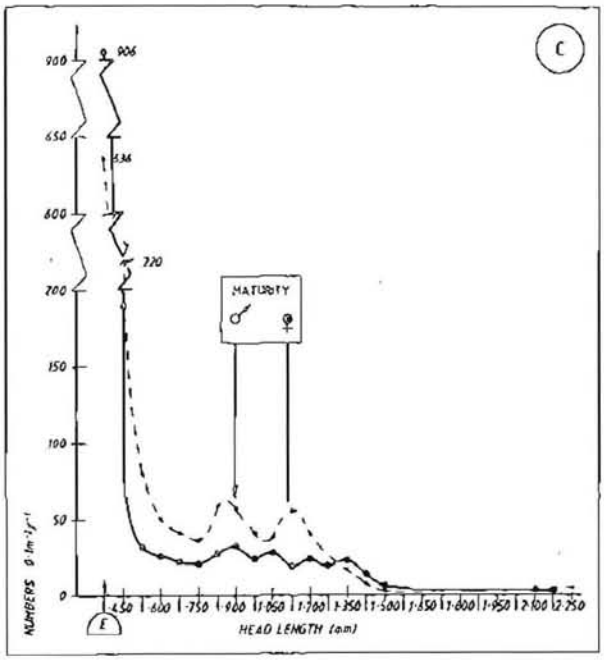

Fig. 12.1C Size-specific survival of female *Patuki*, Oct. 1978 - Oct. 1979 (numbers 0.1 $m^{-2}y^{-1}$). Densities of embryos (E) and juveniles corrected for sex ratio of 1:1.

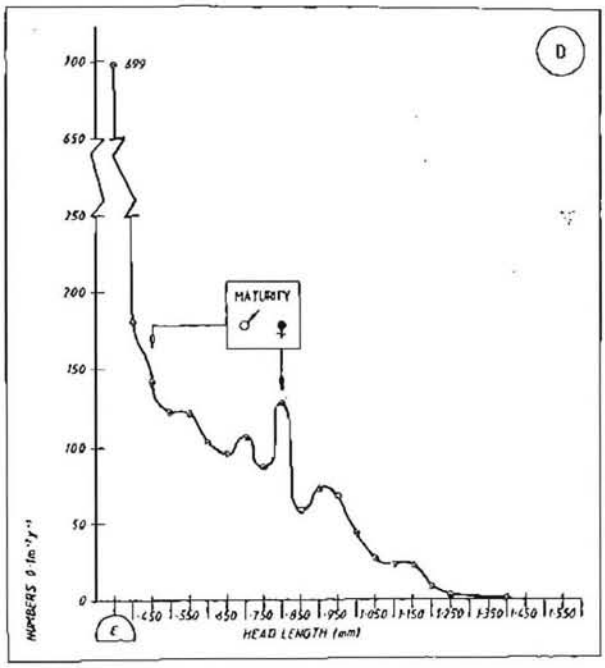

Fig. 12.1D Size-specific survival of female *Paraphoxus*, Oct. 1978 - Sept. 1979 (open circles) and Oct. 1979 - Oct. 1980 (solid circles) (numbers 0.1 $m^{-2}y^{-1}$). Densities of embryos (E) and juveniles corrected for sex ratio of 1:1.

and a few females survive to attain a large size. It is notable that both *Hippomedon* and *Metaphoxus* (type A survival) are small (3.8 and 3.1 mm total length at female maturity) whereas *Paraphoxus* and *Patuki* (type B survival) are larger (6.6 and 6.8 mm total length at female maturity).

From these survival curves it is possible to derive crude estimates of net reproductive rates (R_0) and innate capacities for natural increase (r) to summarize the reproductive performances of each species in South Bay over one year. There are two major sources of error in making these calculations: First, none of the populations had attained a stable age distribution, a prerequisite to the calculation of r, but in reality few populations ever attain this condition. Second, ages of instars were calculated from estimates of ages at maturity (Chapters 5 - 9) using Sutcliffe & Carrick's (1981) relationship for mean moult interval in *Gammarus pulex* at 15°C (mean M_i = $7.5e^{0.008t}$, where t is age (days) from release) for *Hippomedon*, *Metaphoxus* and *Patuki* (Appendix 8.1). For *Paraphoxus*, however, this formula underestimated the number of moult intervals between maturity and the age of older females. Adjustment to the first constant (mean $M_i = 3.8e^{0.008t}$) gave ten moult intervals between 164 and about 434 days corresponding to the predicted number of instars between these ages, and ages of each instar were estimated accordingly (Appendix 8.1). Values of R_0 and r were calculated from the tables in Appendix 8.2 using $r = \log_e R_0/G$ and mean length of generation, $G = \sum l_x m_x X/R_0$ (Krebs, 1978).

It is notable that values of r increase with species mortality risks (Table 12.3); that is, in species with greater mortality risks each individual produces more offspring per unit time than individuals of species with lower mortality risks. *Paraphoxus* seems to be an exception however, since values of r over the two years were very low (<.15). The net reproductive rate (R_0) for this species in both years was also low indicating that the population was only just replacing itself. Density data (Fig. 8.1) suggest that the population did not attain 'normal' densities during the 1979 - 80 summer compared with 1978 - 79, possibly a consequence of the more frequent storms in the second summer (Chapter 3).

Instead of reviewing theories of life-history tactics and their discussions (for recent reviews and discussions see Stearns, 1976, 1977; Bell, 1980), I shall briefly discuss the combinations of traits seen in each

Table 12.3 Estimates of net reproductive rates, R_0, and innate capacities for increase, r, for the five Kaikoura crustaceans.

	R_0	r
Cycloleberis	2.726	.358/.501
Hippomedon	1.457	.945
Paraphoxus	1.106/1.130	.125/.142
Metaphoxus	1.860	1.006
Patuki	1.615	1.112

of these species and then consider how they fit current ideas on life-history tactics.

The *Hippomedon* population is characterized by remarkably consistent seasonal density changes from year to year (very low F, Table 12.1) and low r (Table 12.3) suggesting that density-dependent regulation may be important much of the time. Size-specific survival follows the type A pattern with relatively high recruitment success. Females mature at a fairly young age and small size, produce few, quite large eggs per brood and per lifetime, of which only about 14% are lost before hatching. Here there is an economy of egg production. Few large eggs which probably are easier to hold in the brood pouch and which enhance juvenile fitness and survival are produced rather than more smaller eggs with resultant greater brood and recruitment mortality. The combination of a relatively long lifetime during which eight broods may be raised, the low adult mortality and the high recruitment success means that relatively few cohorts are necessary to ensure continuation of the population at normal densities.

Seasonal densities of the *Metaphoxus* population are rather variable between years resulting in a moderately high value of F (Table 12.1) and the innate capacity for increase (r) is high, both indicating considerable density-independent mortality. Recruitment survival is relatively high (24%) and subsequent population survival follows the type A pattern. Females mature at an intermediate age and small size. They produce few small eggs of which about one third are lost before hatching, thus reducing the effective brood size to less than that of *Hippomedon* (Table 12.2). High recruitment success, high post-recruitment survival, the large number of simultaneous cohorts in the population, and the production of up to seven broods per female compensate for the small brood size, and the few small eggs per brood ensures greater survival of females to breed again.

The high recruitment mortality in both *Patuki* and *Paraphoxus* is offset by their subsequent high survival, the rapid growth of females beyond maturity, and the persistence of a few, very large females that produce large broods (up to 40 and 24 eggs respectively). The standardized brood sizes (eggs per 6 mm long female) (Table 12.2) are very different, however, showing, when the similarity of egg sizes is considered, the large difference in reproductive efforts between the two. *Paraphoxus* matures late, produces abundant large eggs which suffer high mortality whereas there are no losses of the very few, larger eggs produced by the earlier maturing *Patuki*. The significance of these differences is seen in *Patuki's* markedly higher innate capacity for increase (r) (Table 12.3) compared with that for *Paraphoxus*. Thus the reproductive tactics of *Patuki* seem a model of efficiency: The small number of eggs produced all hatch, hatchlings are large affording high fitness and survival, but despite this judicious allocation of resources, the reproductive effort per brood is low thus augmenting female survival to breed again.

It is of interest that *Paraphoxus* and *Patuki* are two extremes in reproductive effort as measured by dry weight of the mean brood as percentage of female dry weight at maturity: *Paraphoxus*, 38.07%; *Patuki*, 10.80% (data Appendix 8.3). The similarity of their survival patterns (both type B) despite *Patuki's* high mortality-risk habitat, indicates that its lower reproductive effort bestows greater female survival and a greater innate capacity for increase. Recently, Lynch (1980) demonstrated a clear negative relationship between reproductive effort and mean life expectancy among nine species of Cladocera. Thus the precept of high reproductive effort - low female survival

(see below and Stearns, 1976) appears true for brooding Crustacea.

How does the large, semelparous *Cycloleberis* compare with these amphipods? Table 4.14 presents instar life tables for two cohorts of *Cycloleberis* from the South Bay population and survival curves taken from these are plotted in Fig. 12.2. Recruitment mortality differs between cohorts (B, 67.6%; C, 97.9%; $\bar{x}$, 82.8%) and post-recruitment survival is high, but 100% mortality occurs in instar VII. This does not fit either of the above two survival patterns principally because of the determinate nature of ostracod growth. Although it is similar to pattern B, another survival pattern (type C) is required for this determinate, semelparous species. The single brood consists of numerous, very large eggs and there is no brood mortality (Table 12.2). Usually only one cohort matures and breeds each year so the success of breeding is important. The large brood size compensates for the single clutch produced at the end of each female's three year lifespan and the very large eggs ensure that hatchlings begin with a high fitness thus minimizing recruitment mortality.

How does each of these combinations of life-history traits conform with predictions of the theories? Stearns (1976: table 4) concisely summarized the expectations of r- and K-selection and of bet-hedging under different conditions (see Table 12.4). One point in this Table requires clarification: Stearns' (1976) table 4 described the two alternatives of bet-hedging as 'adult mortality variable' and 'juvenile mortality variable'. Later he (Stearns, 1977: table 1) adopted more rigorous and unrealistic criteria for these alternatives; 'juvenile mortality or birth rate fluctuates, adult mortality does not' and the converse. Populations in which juvenile mortality (or birth rate) and adult mortality do not fluctuate must be extremely rare. Further, in his foundation study of bet-hedging, Meats (1971) was not concerned with variations in mortality specifically, but rather with the relative intensities of prereproductive mortality and mortality of reproductive (adult) individuals. Similarly, Schaffer (1974a) following Hairston *et al.* (1970) and Pianka (1972), emphasized that the two alternatives were reproductive success (prereproductive or juvenile survival) and adult survival, and reiterated that (pp. 788-789) 'it is the age-specificity of the mortality, constant or fluctuating, that determines the adaptive response' (see also Horn, 1978).

According to these criteria all five South Bay species experience high prereproductive (juvenile) mortality relative to adult mortality, but this is

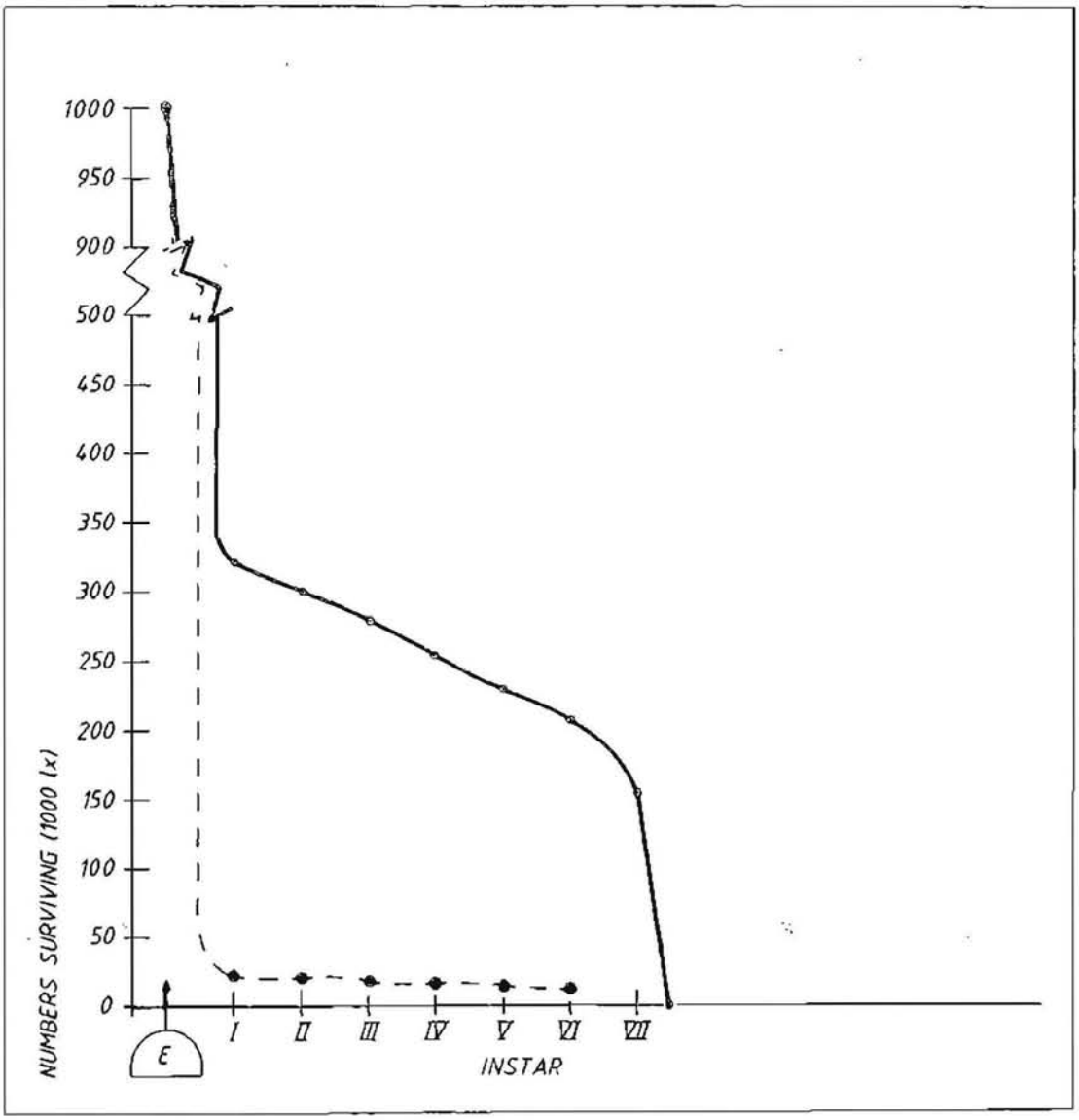

Fig. 12.2 Instar-specific survival patterns of cohorts B (open circles) and C (closed circles) of *Cycloleberis* Oct. 1978 - Oct. 1980 (E, embryos).

Table 12.4 The combinations of life-history traits predicted by r- and K-selection and by bet-hedging (modified from Stearns 1976: table 4).

	Stable environments	Unstable environments
1. r- and K-selection and bet-hedging with high adult mortality	a. slow development late maturity iteroparity smaller reproductive effort fewer young long life	b. rapid development early maturity semelparity larger reproductive effort more young short life
2. Bet-hedging with high juvenile mortality	a. early maturity iteroparity larger reproductive effort shorter life more young per brood fewer broods	b. late maturity iteroparity smaller reproductive effort longer life fewer young per brood more broods

greater in *Paraphoxus*, *Patuki* (type B survival pattern) and *Cycloleberis* (type C survival) than in *Hippomedon* and *Metaphoxus* (type A survival). In addition, ranking of the species from high to low mortality risk corresponds to the order of their ranking on a r - K continuum.

There is poor agreement between the theoretical predictions (Table 12.4) and the observed combinations of life-history traits (Table 12.2). *Cycloleberis*, *Hippomedon* and *Paraphoxus* inhabit relatively more stable habitats and none fits exactly the predictions of r- and K-selection, although *Hippomedon* approaches the criteria for being K-selected (Table 12.4, 1a) except

that it matures early in life. *Cycloleberis* violates the predictions for r-selected species (1b) by maturing late in its long life, and none of the amphipods fulfills all of these conditions, especially that of semelparity. *Metaphoxus* and *Patuki*, inhabitants of the least stable habitats, are short-lived and mature early but their reproductive efforts in terms of brood sizes and numbers of eggs per lifetime are not large.

Hippomedon and *Metaphoxus* populations suffered less juvenile mortality than the other species and could thus be examples of each alternative of the first bet-hedging dichotomy (Table 12.4, 1a and 1b respectively). As discussed above, there is reasonable agreement between *Hippomedon's* combination of life-history traits and the bet-hedging predictions, but *Metaphoxus* does not fit the predictions for fluctuating environments. Perhaps these two species more properly belong in alternative 2 because their juvenile mortalities are higher than their adult mortalities. However, *Hippomedon's* traits differ from those listed under option 2a: it matures early, but reproductive effort and brood size are small, longevity is not notably brief and no fewer broods are produced per lifetime. Similarly, predictions under option 2b are not in close agreement with the combination of traits observed in *Metaphoxus*: Maturity is not late in life, the lifetime is not long and it produces no more broods than other species.

Cycloleberis obviously does not qualify for option 2a because it matures late, it is semelparous, and it is long-lived. *Paraphoxus* matures late in its long lifetime and produces more broods per life-time than the other amphipods and so does not conform to the combination of traits under 2a. Nor does it fit the scheme for fluctuating environments (2b) any better; reproductive effort is greater and brood size is larger. The remaining species, *Patuki*, is expected to possess the combination of traits predicted for fluctuating environments (2b), but again several points do not concur. *Patuki* does not mature late in life, its lifetime is brief and it produces no fewer broods than most other species.

It may be argued that relative egg size (egg length/length of smallest reproductive female) is a more correct measure of egg size. However when this is substituted for absolute egg size in Table 12.2, there is no appreciable improvement between observed combinations of traits and the theoretical predictions.

Why do both theories fail so badly in predicting the combinations of traits seen in these crustaceans? Part of the problem almost certainly lies in the difficulty of comparing such characteristics between species. For example, how should two species be ranked according to length of life when they are of quite different size and their populations exhibit different patterns of survival? An example seen here is the comparison of *Metaphoxus* and *Paraphoxus*, and perhaps even more difficult to reconcile is the problem of equating length of life for species with indeterminate growth and species with determinate growth (e.g. *Patuki* and *Cycloleberis*). Further, the positive correlation between eggs per brood and female size described for many amphipods illustrates the need for adjusting brood size or number of young to compensate for female size. Quantification of reproductive effort in terms of energy expenditure seems an excellent parameter for comparisons but it is time-consuming, often impractical and has been rarely estimated (Christiansen & Fenchel, 1979).

The principal reason for the failure of these theories is that they have been devised with little regard to the organisms to which they are intended to apply. Stearns (1977) discussed 'design constraints' which 'may keep populations from reaching their predicted optima' but apparently failed to comprehend the magnitude of this limitation, at least in some marine crustaceans. Christiansen & Fenchel (1979) touched on this phenomenon briefly, describing it as 'evolutionary indeterminism', the 'most important reservation that must be made in any evolutionary model'. Others also were aware of this difficulty (Spight, 1979) and, noting that such constraints differ between phylogenetic groups, Reaka (1979) and Lynch (1980) considered that an appropriate analysis of the adaptive values of different life histories is to compare closely related species exposed to different selection pressures. I fully agree and prefer the term 'phylogenetic constraint' to describe the limitation of a particular trait, morphological or physiological, which is cosmopolitan within a taxon and rigidly imposed by the irreversible loss of viable genetic alternatives for the trait. Excellent examples of phylogenetic constraints are seen here: Gammaridean amphipods and ostracods of the order Myodocopida are exclusively brooders and myodocopids are semelparous. Obviously these constraints differ between phylogenetic groups and within a group of organisms there may be a heirarchy of taxon-related phylogenetic constraints. Among the Crustacea, amphipods have adopted the brooding habit, most are iteroparous except members of the family Ampeliscidae which are semelparous (Nelson, 1980;

Hastings, 1981; Wildish, 1982). Further, among iteroparous families brood mortality seems to be low (<15%) in the Lysianassidae, and one of its genera has adopted sex reversal as a normal life-history trait (Lowry *et al.*, in prep.). Similar examples occur in many groups of organisms and Spight (1979) pointed out that several life-history characteristics can be predicted when only the major taxon of the organism is known. Traditionally we accept many morphological similarities (or a common lack of genetic alternatives for given morphological characters) as important taxonomic criteria and there is no reason to suppose that various life-history traits are not similarly taxon-related or phylogenetically constrained. Indeed some reproductive traits may be a consequence of certain morphological features.

The presence of phylogenetic constraints on some life-history traits by no means implies that a given taxon is necessarily restricted to habitats with certain stability characteristics: Rather, the genetic diversity of other life-history traits will determine the range of habitats available to units (species) of the taxon. That is, the unconstrained life-history traits will be coadapted with each other and with the constrained traits to compensate for the restriction of the phylogenetically constrained traits. Implicit in this hypothesis is the concept that there is no single optimum life history, but that different combinations of life-history traits may be equally successful in a given environment.

A heirarchical scheme incorporating the various taxon-related phylogenetic constraints at higher levels seems a reasonable alternative means of studying the evolution of life-history tactics among related species. At levels below the fixed traits, the unconstrained traits are expected to be coadapted to produce a successful tactic, a combination of traits that ensures adquate current and future reproduction through the differential age-specific allocation of energy to maintenance (survival), growth and reproduction in order to maximize the overall genetic contribution to subsequent breeding populations. Two principles are the basis for predicting the behaviour of each trait in promoting the optimal tactic: 1. There is a real cost (in maintenance and/or growth) to the parent associated with reproduction and greater reproductive effort reduces the probability of surviving to reproduce again (Williams, 1966; Murphy, 1968; Tinkle, 1969; Gadgil & Bossert, 1970; Gadgil & Solbrig, 1972; Menge, 1974; Schaffer, 1974b; Pianka & Parker, 1975; Lynch, 1980; and see Stearns, 1976 for review). 2. Large offspring or large hatchlings from large

eggs are ecologically fitter and thus more likely to survive than small offspring or hatchlings from small eggs (Thorson, 1950; Smith & Fretwell, 1974; Spight, 1976; Todd & Doyle, 1981).

As a result of his work on two species of *Thias* (a genus of muricid prosobranch gastropods), Spight (1979) similarly suggested that life-history characteristics should be listed in three heirarchical levels: those with a fairly small range (traits characteristic of the family Muricidae), those with moderate ranges but smaller than the range for other prosobranchs, and characteristics encompassing the range found among the subclass Prosobranchia. There seems no necessity for a universal three-level scheme and indeed the number of levels and the taxonomic groups (subclass, order, family) within each level is likely to differ from group to group.

Table 12.5 offers the beginnings of a heirarchical scheme of life-history traits for the five species examined here; the beginnings of a scheme because as yet we know very little of the life histories of gammaridean amphipods and myodocopid ostracods with the result that many phylogenetic constraints and their distribution among taxa are poorly known. Brood mortality should perhaps be elevated in the heirarchy since evidence suggests that for amphipods it is a familial character in part, not simply a specific character (Chapter 9). Note that among the amphipods from each habitat type (relative stability), survival pattern and female size at maturity are correlated, and that the former almost certainly is a consequence of the latter because brood size (Steele & Steele, 1975a; Nelson, 1980; Van Dolah & Bird, 1980; Moore, 1981; present study, Chapter 9) and egg size (Nelson, 1980; present study, Chapter 9, Fig. 9.2) are both significantly correlated with female size in the Gammaridea. In myodocopids adult female length is significantly correlated with brood size (Chapter 4) but too few data are available on the relationship between egg size and female size. Correlations between body size and specific life-history traits appear widespread among Crustacea. Body size (median length and volume) of gonadactylid stomatopods is significantly and positively correlated with egg diameter, egg volume, mean egg number per clutch and per lifetime, juvenile settling size and growth rate, and negatively correlated with age at maturity (Reaka, 1979). Cladocera also show significant positive correlations between body size and egg size, clutch size, age at maturity and mean lifespan (Lynch, 1980). Body size thus explains much of the diversity of these life-history traits but the relationships are usually broad and species

Table 12.5 A heriarchical scheme of life-history tactics of the Kaikoura crustaceans.

Trait	brooding habit					
	iteroparous				semelparous	
habitat	more stable		less stable		more stable	less stable
survival pattern	type A	type B	type A	type B	type C	
example	*Hippomedon*	*Paraphoxus*	*Metaphoxus*	*Patuki*	*Cycloleberis*	No examples from this study
female size	small	large	small	large	very large	
female maturity	early	late	intermediate	intermediate	very late	
brood size	small	large	small	very small	very large	
brood mortality	moderate	high	high	nil	nil	
egg size	small	moderate	very small	large	very large	
maximum longevity	moderate	long	brief	very brief	very long	
relative egg size	large	small	very large	small	extremely large	

with similar body sizes may differ appreciably with respect to individual traits. Despite these differences and in view of the correlations of 'traditional' traits with body size, more emphasis should be given to the prediction of other life-history traits such as age at maturity, number of broods per lifetime, size/age-specific mortality and natality. Such traits have been determined for only a few species of amphipods (Sexton, 1928; Myers, 1971; Nair & Anger, 1979a,b) and require extensive laboratory rearing of individuals. Thus a new approach to the evolution and prediction of life-history traits of brooding Crustacea (and probably most other organisms also) is essential, a more flexible approach that recognizes phylogenetic constraints and the possibility of several equally successful combinations of traits for a given situation.

Such an approach is Lynch's (1980) synthesis of the life-history tactics of Cladocera. His ideas on optimal body size brought together information on size-specific foraging efficiencies, size-specific mortality (principally predation), size-specific growth rates and size-specific reproductive efforts. Briefly, species growth patterns have evolved to balance optimal foraging size against size-specific mortality on one hand the demands of reproduction on the other. As with amphipods, cladoceran life histories are governed by several phylogenetic constraints; cladocerans are iteroparous and female size is related to brood size, egg size, size at maturity and mean lifespan. Lynch's approach demonstrates that there is far more to their life-history tactics than simply age at maturity, longevity and number of broods. Future studies of life-history tactics require a broader outlook to beyond simple life history and population parameters. Unfortunately the study of amphipod and ostracod biologies lags so far behind knowledge of cladocerans that we cannot begin to apply his ideas to these animals.

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Appendix 1.1 Instar frequency of *Cycloleberis zealandica* taken in a single plankton tow off the New Wharf, Kaikoura, at c.a. 2030 h, 8 May 1980.

Instar	Sex	Numbers	Remarks
I	juv.	2	
II	juv.	7	
III	juv.	5	
IV	juv.	10	
V	♂	10	
	♀	7	
VI	♂	6	
	♀	4	
VII	♂	21	All with elongate antenna 2, elongate carapace and posterior fringe of fine setae.
	♀	12	Three with 38 (stage 3), 39 (stage 2), 40 (stage 1) embryos.

Appendix 2.1 Summary of experiments to determine embryonic development times and growth rates for *Hippomedon*.

Growth expt, 4 July - 5 Oct. 1979, E.P.F.S.

4 July 1979: 31 individuals of known size placed in mesh cages with a small quantity of sand and held in running seawater

11 Aug. 1979: 3 individuals grown from 0.400 to 0.425 mm h.l., 1 grown from 0.350 to 0.375 mm h.l., 5 individuals died.

7 Sept. 1979: 1 individual grown from 0.400 to 0.425 mm h.l., 1 grown from 0.400 to 0.450 mm h.l., 1 female (0.450 mm h.l.) produced 4 juveniles (all 0.225 mm h.l.), 7 individuals died.

5 Oct. 1979: No growth recorded, all but 4 individuals were dead. Experiment abandoned.

Growth expt, 8 Dec. 1979 - 18 Feb. 1980, E.P.F.S.

8 Dec. 1979: 15 individuals of known size placed in mesh cages containing a small quantity of sand and held in running seawater.

18 Dec. 1979: Another 19 individuals added to this expt.

17 Jan. 1980: First group - 1 individual grown from 0.400 to 0.450 mm h.l., all others dead.

Second group - no growth recorded, all but 4 dead.

18 Feb. 1980: Remaining 4 individuals dead and no growth recorded.

Embryonic development rate expt, 8 - 18 Nov. 1980, Zoology Department.

8 Nov. 1980: 11 gravid females examined for state of brood development. Even with strong illumination reflected from beneath the animal held on its side; it was difficult to detect brood contents and impossible to determine the state of embryonic development. Females were placed in separate cages containing a small amount of sand, immersed in filtered seawater, and held at 15°C with continuous aeration.

10 Nov. 1980: All alive, no broods released. Water changed.

12 Nov. 1980: 3 dead, no juveniles released. Water changed.

16 Nov. 1980: Another 4 dead, no juveniles released. Water changed.

18 Nov. 1980: Remaining 3 dead, no juveniles released.

Appendix 2.2 Monthly differences in mean egg (stage 1 embryo) lengths in *Hippomedon*.

	length (mm)			significance	
	$\bar{x}$	SD	n	t	p
Oct. 1978	.450	.032	6		
				2.271	.05 - .02
Nov.	.418	.023	19		
				.908	n.s.
Dec.	.410	.038	29		
				1.417	n.s.
Jan. 1979	.400	0	3		
				3.106	.05 - .02
Feb.	.425	.018	5		
				.927	n.s.
Mar.	.432	.019	7		
				.540	n.s.
Apr.	.440	.029	5		
				1.012	n.s.
Apr.	.425	0	2		
				1.583	n.s.
May	.444	.024	4		
				2.545	.05 - .02
July	.479	.033	12		
				1.609	n.s.
Aug.	.661	.695	38		
				2.162	.05 - .02
Sept.	.417	.021	21		
				3.098	.01 - .001
Oct.	.434	.023	58		
				6.770	<.001
Nov.	.445	.019	15		
				3.008	.01 - .001
Dec.	.406	.024	4		
				4.969	.01 - .001
Jan. 1980	.479	.019	6		
Feb.	-	-	-		
				2.707	.05 - .02
Mar.	.500	0	1		

Appendix 2.3 Seasonal differences in mean length of eggs (stage 1 embryos) for *Hippomedon*.

	1978		1979			1980
	Spring (Oct.-Nov.)	Summer (Dec.-Feb.)	Autumn (Mar.-May)	Winter (June-Aug.)	Spring (Sept.-Nov.)	Summer (Dec.-Feb.)
Egg length (mm)						
$\bar{x}$	.428	.412	.436	.451	.432	.450
SD	.028	.034	.021	.059	.024	.043
n	27	37	18	39	94	10
significance / t, dfs						
Spring		p<.05	n.s.	p<.05	n.s.	n.s.
Summer	2.061,62		p<.01	p<.001	p<.01	p<.02
Autumn	1.093,43	3.215,53		n.s.	n.s.	n.s.
Winter	2.115,64	3.553,74	1.781,55		n.s.	n.s.
Spring	.675,119	3.272,129	.723,110	1.945,131		n.s.
Summer	1.504,35	2.585,45	.968,26	.060,47	1.302,102	

Appendix 2.4 Seasonal mean (± SE) brood sizes for broods at development stages 1 - 5 and seasonal brood mortality for *Hippomedon*.

	Development Stage					
	1	2	3	4	5	% mortality
Oct.-Nov.1978	3.5 ± 1.57	4.07 ± 1.69	3.55 ± 1.29	1.75 ± .96	2.38 ± .92	41.5
	n = 12	n = 14	n = 11	n = 4	n = 8	2-5
			t = 3.036	p <.02		
Dec.1978-Feb.1979	4.13 ± 1.71	4.14 ± 1.79	3.6 ± 1.35	4.33 ± .58	1.71 ± .76	0
	n = 16	n = 14	n = 10	n = 3	n = 7	2-4
Mar.-May	2.38 ± 1.02	3.0 ± 1.41	3.8 ± 1.79	1.67 ± 1.03	1.0	56.1
	n = 16	n = 5	n = 5	n = 6	n = 1	3-4
			t = 2.356	p <.05		
July-Aug.	2.32 ± 1.11	2.85 ± .90	2.0 ± .82	2.0	1.0	29.8
	n = 19	n = 13	n = 7	n = 1	n = 1	2-4
			t = 3.405	p <.01		
Sept.-Nov.	3.68 ± 1.43	4.43 ± 1.09	4.45 ± 1.57	3.8 ± .94	3.0 + 1.68	14.6
	n = 34	n = 14	n = 11	n = 15	n = 13	3-4
			t = 1.222	ns		
Dec.1979-Feb.1980	3.25 ± 1.89	3.41 ± 1.58	3.56 ± 1.24	3.39 + 1.26	2.14 + 1.68	4.8
	n = 4	n = 17	n = 9	n = 13	n = 7	3-4
			t = 0.314	ns		

Appendix 2.5 Mean sizes of broods at each stage of development and brood mortality for different sized female *Hippomedon*.

Female Size (mm h.l.)	Development Stage 1	2	3	4	5	% mortality
.350	1.0 ± 0 n = 2	1.0 ± 0 n = 1	2.2 ± 1.095 n = 5	- n = 0	- n = 0	-
.375	2.0 ± .577 n = 7	2.25 ± .463 n = 8	3.50 ± 2.121 n = 2	2.250 ± 1.50 n = 4	1.50 ± .707 n = 2	35.7 3-4
.400	2.316 ± 1.0 n = 19	3.0 ± 1.564 n = 10	3.0 ± 1.369 n = 17	1.750 ± .957 n = 4	2.143 ± 1.069 n = 7	40.0 2-5
.425	3.455 ± 1.371 n = 33	3.90 ± 1.155 n = 30	3.364 ± 1.093 n = 22	3.111 ± 1.167 n = 9	2.313 ± 1.015 n = 16	20.2 2-4
.450	3.667 ± 1.354 n = 21	4.389 ± 1.501 n = 18	4.750 ± 2.376 n = 8	3.923 ± 1.441 n = 13	2.50 ± 1.414 n = 8	17.4 3-4
.475	4.889 ± 1.616 n = 9	4.182 ± 1.779 n = 11	4.750 ± .886 n = 8	3.429 ± .535 n = 7	2.667 ± 1.862 n = 6	27.8 3-4
.500	4.0 ± 2.345 n = 5	- n = 0		5.0 ± 1.414 n = 2	4.50 ± 3.536 n = 2	-

Appendix 3.1 Summary of experiments to estimate embryonic development times and growth rates for *Patuki*.

Growth expt, 4 July 1979 - 6 Oct. 1979, E.P.F.S.

4 July 1979: 18 individuals measured and placed in individual mesh cages each containing a small amount of sand and held in running seawater.

11 Aug. 1979: Four individuals increased in size (h.l., mm): .750 to .875 mm, 1.000 to 1.025 mm, 1.000 to 1.050 mm, 1.000 to 1.075 mm. This last individual was a female and had released 10 juveniles, all .375 mm h.l. Another female (1.000 mm h.l.) produced 6 juveniles of this size. Nine of the original individuals had died.

8 Sept. 1979: All but 3 individuals dead; no growth.

6 Oct. 1979: All but 1 individual dead; no growth recorded. Experiment terminated.

Growth expt, 8 Dec. 1979 - 29 Aug. 1980, E.P.F.S.

8 Dec. 1979: 10 known-size individuals placed in mesh cages as above.

17 Jan. 1980: All dead, no growth recorded.

Embryonic development rate expt, 4 - 16 Nov. 1980, Zoology Dept.

4 Nov. 1980: State of brood development recorded for 15 gravid females placed individually in mesh cages immersed in seawater and maintained at 15°C. Some died or lost their embryos during the experiment but results gained are tabulated over.

Appendix 3.1 continued. State of embryonic development with time.
(D = ♀ dead, R = juveniles released).

Individual no.	Day 1	2	3	4	5	6	7	8	9
146	3	3	3		4		4D		
147	1	1	2		2D				
73	4	4		5		R			
77	3	3		4		4D			
97	1	2		3		3D			
166	1	2		2		3		3	D
175	3	3		4		4D			
86	1	2		3		3D			

Appendix 3.2 Monthly differences in mean egg (stage 1 embryo) lengths for *Patuki*.

	length (mm)			Significance	
	$\bar{x}$	SD	n	t	p
Oct. 1978	.552	.027	12		
				.289	n.s.
Nov.	.558	.014	3		
				5.788	<<.001
Dec.	.469	.037	8		
				.074	n.s.
Jan. 1979	.490	.022	5		
				1.276	n.s.
Feb.	.506	.022	8		
				2.034	<.05
Mar.	.488	.028	44		
				2.949	<.01
Apr.	.508	.013	6		
				.911	n.s.
Apr.	.492	.029	3		
May	-	-	-		
				3.550	<.05
July	.558	.014	3		
				2.196	<.05
Aug.	.536	.034	33		
				.781	n.s.
Sept.	.529	.033	24		
				2.485	<.02
Oct.	.551	.034	35		
				1.301	n.s.
Nov.	.541	.027	28		
				.189	n.s.
Dec.	.544	.045	9		
				1.270	n.s.
Jan.	.571	.050	11		
				.233	n.s.
Feb.	.567	.020	6		

Appendix 3.3 Seasonal differences in mean egg (stage 1 embryos) lengths for *Patuki*.

	1978		1979			1980
	Spring (Oct.-Nov.)	Summer (Dec.-Feb.)	Autumn (Mar.-May)	Winter (June-Aug.)	Spring (Sept.-Nov.)	Summer (Dec.-Feb.)
egg length (mm)						
$\bar{x}$	.553	.488	.491	.538	.542	.560
SD	.025	.032	.027	.033	.033	.042
n	15	21	53	36	87	27
significance / t, dfs						
Spring		<.001	<.001	n.s.	n.s.	n.s.
Summer	6.835,34		n.s.	<.001	<.001	<.001
Autumn	8.328,66	0.379,72		<.001	<.001	<.001
Winter	1.769,49	5.625,55	7.085,87		n.s.	.02-.05
Spring	1.494,100	6.898,106	9.950,138	0.0617,121		.02-.05
Summer	0.677,40	6.741,46	7.759,78	2.250,61	2.040,112	

Appendix 3.4 Seasonal mean (± SE) brood sizes at stage 1 - 5 and seasonal brood mortality for *Patuki*.

	Development stage					
	1	2	3	4	5	% mortality
Oct.-Nov. 1978	7.2 ± 3.7 n = 5	- n = 0	24.0 n = 1	- n = 0	- n = 0	-
Dec.1978-Feb.1979	3.17 ± 1.99 n = 12	6.15 ± 4.08 n = 13	3.14 ± 1.35 n = 7 t = 3.531	2.0 ± .71 n = 5 p <.01	1.0 n = 1	67.5 2-4
Mar.-May	4.15 ± 2.32 n = 20	4.13 ± 2.36 n = 8	4.67 ± 1.94 n = 9	5.14 ± 4.06 n = 7	4.25 ± .96 n = 4	0 2-4
July-Aug.	7.56 ± 2.74 n = 9	8.43 ± 3.69 n = 7	6.33 ± 4.10 n = 12 t = 0.623	7.25 ± 3.62 n = 8 n.s.	3.75 ± 1.26 n = 4	14.0 2-4
Sept.-Nov.	9.1 ± 4.69 n = 30	9.91 ± 4.42 n = 22	12.25 ± 5.69 n = 12 t = 1.055	10.0 ± 4.30 n = 10 n.s.	10.0 n = 1	18.4 3-4
Dec.1979-Feb.1980	4.1 ± 1.66 n = 10	4.89 ± 3.81 n = 27	5.29 ± 2.95 n = 17	9.13 ± 5.22 n = 8	3.0 n = 1	0 3-4

Appendix 3.5 Mean sizes of broods at each stage of development and brood mortality for different sized female *Patuki*.

Female size (mm h.l.)	Development stage 1	2	3	4	5	% mortality
.850	2.0 ± 0	2.75 ± 1.04	3.43 ± 1.27	1.67 ± .58	-	51.3
	n = 1	n = 8	n = 7	n = 3	n = 0	3-4
.900	3.82 ± 3.19	3.53 ± 1.74	4.0 ± 1.41	3.38 ± 1.60	1.0 ± 0	15.5
	n = 17	n = 17	n = 13	n = 8	n = 1	3-4
.950	5.38 ± 2.68	5.0 ± 2.26	5.06 ± 2.27	4.88 ± 1.16	3.33 ± 2.08	3.6
	n = 16	n = 12	n = 16	n = 9	n = 3	3-4
1.000	7.17 ± 4.35	6.33 ± 3.28	6.13 ± 2.53	4.86 ± 1.77	4.67 ± .58	32.2
	n = 12	n = 12	n = 8	n = 7	n = 3	1-4
1.050	9.14 ± 3.98	8.0 ± 3.20	12.20 ± 5.02	7.63 ± 3.93	4.0 ± 0	37.5
	n = 7	n = 9	n = 5	n = 8	n = 1	3-4
1.100	8.82 ± 4.07	9.70 ± 2.31	10.71 ± 4.46	8.40 ± 4.83	3.0 ± 0	21.5
	n = 11	n = 10	n = 7	n = 5	n = 1	3-4
1.150	11.13 ± 5.54	14.83 ± 4.71	10.0 ± 4.0	13.67 ± .58	-	7.8
	n = 8	n = 6	n = 3	n = 3	n = 0	2-4
1.200	6.20 ± 2.59	12.33 ± 4.16	19.33 ± 5.69	12.0 ± 6.06	-	37.9
	n = 5	n = 3	n = 3	n = 4	n = 0	3-4
1.250	11.0 ± 0	16.0 ± 0	11.67 ± 7.77	17.0 ± 0	10.0 ± 0	0
	n = 1	n = 1	n = 3	n = 1	n = 1	2-4

Appendix 4.1 Summary of experiments to estimate growth rates and embryonic development times for *Metaphoxus littoralis*.

Growth expt, 8 Dec. 1979 - 30 May 1980, E.P.F.S.

8 Dec. 1979: 7 individuals measured and placed in small mesh cages containing sand and immersed in running seawater.

18 Dec. 1979: Another 6 individuals added to the expt.

17 Jan. 1980: 2 individuals had died, 1 female had produced a brood of juveniles, 1 female grew from 0.750 to 0.825 mm h.l. since 8 Dec. 1979. A further 7 individuals added to the expt.

18 Feb. 1980: 5 individuals were dead, the female above grew to 0.875 mm h.l., 1 grew 0.050 mm h.l. to 0.750 mm h.l. since 17 Jan. 10 more individuals added to the expt.

20 Mar. 1980: 13 dead, 3 individuals increased in size by 0.025 mm h.l. to 0.525 mm h.l. and 2 to 0.800 mm h.l., 1 grew from 0.675 to 0.750 mm h.l. since 18 Feb., remaining individuals showed no growth.

19 Apr. 1980: 9 dead, of the 3 remaining, 1 grew 0.625 to 0.725 mm h.l. and another grew from 0.750 to 0.775 mm h.l.

30 May 1980: 2 dead, remaining individual had not grown.

Embryonic development rate expt, 4 - 16 Nov. 1980, Zoology Dept.

Twelve gravid females separated into mesh cages and the state of their broods recorded as over:

State of embryonic development with time (D = ♀ dead, R = juveniles released, E = brood pouch empty and no juveniles present).

	Day								
Female no.	1	3	4	6	7	8	9	10	11
163	2-3	D							
170	2-3		early 4	4	E				
6	4	4	5 part R	5		5			
7	3	early 4	4	4		5	5 part R		R
8	1-2	2	3	3		E			
81	1-2	1-2	2	2D					
84	1-2	1-2	1-2	2-3		2-3	2-3	E	
85	4	5	5	R					
91	5	5	R						
92	3	early 4	4	4		5	5		R
51	1-2	1-2	2	2-3		3	E		
64	2-3	3	3	3		3	3		D

Appendix 4.2 Monthly differences in mean egg (stage 1 - 2 embryos) lengths for *Metaphoxus littoralis*.

	Length (mm)			Significance	
	$\bar{x}$	SD	n	t	p
Nov. 1978	.390	.028	15		
				2.294	<.05
Dec.	.346	.047	7		
				1.001	n.s.
Jan. 1979	.371	.043	6		
				0.068	n.s.
Feb.	.369	.047	4		
				0.122	n.s.
Mar.	.372	.032	19		
				0.153	n.s.
Apr.	.369	.063	12		
				0.731	n.s.
Apr.	.383	.018	9		
				0.964	n.s.
May	.375	.025	19		
				1.017	n.s.
July	.387	.046	16		
				1.333	n.s.
Aug.	.370	.034	38		
				0.269	n.s.
Sept.	.368	.039	61		
				0.853	n.s.
Oct.	.374	.035	50		
				1.985	n.s.
Nov.	.390	.036	32		
				0.473	n.s.
Dec.	.386	.030	29		
				1.403	n.s.
Jan. 1980	.410	.032	15		
				0.454	n.s.
Feb.	.406	.013	18		
				0.434	n.s.
Mar.	.408	.015	19		

Appendix 4.3 Seasonal differences in mean egg (stages 1 - 2) lengths for *Metaphoxus littoralis*.

	1978		1979			1980
	Spring (Oct.-Nov.)	Summer (Dec.-Feb.)	Autumn (Mar.-May)	Winter (June-Aug.)	Spring (Sept.-Nov.)	Summer (Dec.-Feb.)
Egg length (mm)						
$\bar{x}$	.382	.360	.373	.375	.375	.398
SD	.032	.044	.036	.039	.037	.028
n	18	17	61	54	144	61

probability / t, dfs						
Spring		n.s.	n.s.	n.s.	n.s.	n.s.
Summer	1.684,33		n.s.	n.s.	n.s.	<.001
Autumn	1.018,77	1.118,76		n.s.	n.s.	<.001
Winter	0.759,70	1.259,69	0.285,113		n.s.	<.001
Spring	0.859,160	1.350,159	0.361,203	0,198		<.001
Summer	1.916,77	3.375,76	4.281,120	3.591,113	4.864,203	

Appendix 4.4 Seasonal mean (± SE) brood size at stages 1 - 5 and seasonal brood mortality for *Metaphoxus littoralis*.

	Development stage					
	1	2	3	4	5	% mortality
Oct.-Nov. 1978	3.14 ± 1.86 n = 7	6.0 n = 1	3.0 ± 1.58 n = 5	1.0 n = 1	1.0 n = 1	83.3
Dec.1978-Feb.1979	3.0 ± 2.83 n = 2	2.5 ± 1.23 n = 6	1.0 n = 1	1.0 ± 0 n = 2	- n = 0	66.7 1-4
Mar.-May	2.38 ± 1.31 n = 16	1.73 ± .96 n = 15	2.86 ± 1.35 n = 7	1.11 ± .33 n = 9	2.0 n = 1	30.1 3-5
July-Aug.	2.07 ± 1.28 n = 15	2.67 ± 1.72 n = 12	2.17 ± 1.70 n = 12	1.86 ± .90 n = 7 t = 1.346 ns	- n = 0	30.3 2-4
Sept.-Nov.	3.17 ± 1.90 n = 36	3.17 ± 1.55 n = 24	3.24 ± 1.20 n = 17	2.31 ± 1.20 n = 16 t = 2.225 p <.05	1.5 ± 1.0 n = 4	28.7 3-4
Dec.1979-Feb.1980	3.73 ± 2.12 n = 15	2.85 ± 1.91 n = 13	3.11 ± 1.82 n = 19	2.0 ± 1.23 n = 9 t = 0.803 ns	2.67 ± 2.08 n = 3	28.4 1-5

Appendix 4.5 Mean sizes of broods at each stage of development and brood mortality for different sized female *Metaphoxus littoralis*.

Female size (mm h.l.)	Development stage 1	2	3	4	5	% mortality
.600	1.40 ± .52	1.23 ± .60	1.55 ± .69	1.13 ± .35	-	27.1
	n = 10	n = 13	n = 11	n = 8	n = 0	3-4
.650	1.64 ± .84	1.40 ± .50	1.67 ± 1.32	1.42 ± .90	1.50 ± .71	10.2
	n = 14	n = 20	n = 9	n = 12	n = 2	3-5
.700	2.77 ± 1.45	3.0 ± 1.24	2.46 ± 1.13	1.92 ± .90	1.50 ± .71	36.0
	n = 26	n = 23	n = 13	n = 12	n = 2	2-4
.750	3.31 ± 1.86	3.62 ± 1.66	3.18 ± 1.44	2.30 ± 1.25	1.67 ± 1.16	36.5
	n = 32	n = 13	n = 22	n = 10	n = 3	2-4
.800	3.63 ± 1.51	3.38 ± 1.60	4.0 ± 1.27	2.75 ± 1.71	3.0 ± 2.83	25.0
	n = 8	n = 8	n = 6	n = 4	n = 2	3-5
.850	5.0 ± 3.03	5.25 ± 1.71	4.0 ± 1.92	2.0 ± 0	-	61.9
	n = 6	n = 4	n = 7	n = 1	n = 0	2-4

Appendix 5.1 Summary of growth rate and embryonic development time observations on *Paraphoxus*.

Growth expt, 4 July 1979 - 6 Oct. 1979, E.P.F.S.

Ten individuals observed of which 4 survived longer than 1 month and grew:

individual	increment (mm h.l.)	time (days)	growth rate (mm 30 days^{-1})
1	.100	56	.0536
2	.150	56	.0804
3	.250	67	.1119
4	.025	39	.0192
	$\bar{x}$ = .0663 SD = .0394 n = 4		

Growth expt, 8 Dec. 1979 - 28 Aug. 1980, E.P.F.S.

Thirty-three individuals observed, most survived for at least 1 month but only 11 increased in size:

individual	increment (mm h.l.)	time (days)	growth rate (mm 30 days^{-1})
16	.300	133	.0677
29	.100	40	.0750
31	.050	30	.0500
32	.150	31	.1450
33	.225	93	.0726
34	.100	71	.0423
36	.100	123	.0244
39	.100	63	.0476
41	.350	93	.1129
42	.075	71	.0317
52	.175	123	.0427
	$\bar{x}$ = .0647 SD = .0363 n = 11		

Both expts produced a similar rate (t = .0710, n.s.) so results combined to produce an overall mean growth rate of 0.0651 mm 30 days^{-1}(SD = 0.0357, n = 15).

Embryonic development rate expt, 5 Nov. - 21 Dec. 1980, Zoology Dept.

Broods of six gravid females were examined and their state of development recorded. Females were held in individual mesh cages immersed in aerated seawater and maintained at 15°C. Development was recorded at intervals as below:

individual	Day 1	2	3	4	5	6	7	8	9	10	11	12	13	14
74	5		all released											
98	2		3	4		4		4	5			all released		
153	1		2	2		2		2-3	2-3			3		4-5
155	early 4		5	5 2 released			all released							
161	5		all released											
163	2-3		3	4			4		5					

Estimated duration of development from stage 2 to release of juveniles c.a. 17 - 21 days at 15°C. Allowing 2 - 3 days for stage 1, then entire embryonic development period must be within 19 - 24 days.

Appendix 5.2 Seasonal mean egg (stage 1 embryo) lengths for *Paraphoxus*.

Egg length (mm)	1978 Spring (Oct.-Nov.)	1978 Summer (Dec.-Feb.)	1979 Autumn (Mar.-May)	1979 Winter (July)	1979 Spring (Sept.-Nov.)	1979 Summer (Dec.-Jan.)	1979 Autumn (Mar.-May)	1980 Winter (July-Aug.)	1980 Spring (Oct.)
$\bar{x}$	.497	.461	-	.479	.508	.538	-	.513	.524
SD	.036	.033	-	.019	.037	.029	-	.051	.048
n	58	9	0	6	21	21	0	12	9
significance / t, dfs									
Spring		<.01	-	n.s.	n.s.	<.001	-	n.s.	n.s.
Summer	3.007,65		-	n.s.	<.01	<.001	-	<.02	<.01
Autumn	-	-		-	-	-	-	-	-
Winter	1.982,62	1.337,13	-		<.02	<.001	-	n.s.	<.05
Spring	1.176,77	3.444,28	-	2.590,25		<.01	-	n.s.	n.s.
Summer	5.191,77	6.068,28	-	5.894,25	2.924,40		-	n.s.	n.s.
Autumn	-	-	-	-	-	-		-	-
Winter	1.035,68	2.830,19	-	2.043,16	0.298,31	1.560,31	-		n.s.
Spring	1.618,65	3.245,16	-	2.531,13	0.102,28	0.814,28	-	0.506,19	

Appendix 6.1 Mean sediment depths inhabited by males and females of each instar in ripples and in troughs (dfs = 12 in all cases).

P / t	IV crests ♂	IV crests ♀	IV troughs ♂	IV troughs ♀	V crests ♂	V crests ♀	V troughs ♂	V troughs ♀	VI crests ♂	VI crests ♀	VI troughs ♂	VI troughs ♀
IV crests ♂		ns	ns	ns								
IV crests ♀	.397		ns	ns								
IV troughs ♂	.514	1.123		ns								
IV troughs ♀	.634	.357	1.156									
V crests ♂						ns	ns	ns				
V crests ♀					.076		ns	ns				
V troughs ♂					.949	.967		ns				
V troughs ♀					.752	.776	.113					
VI crests ♂										ns	ns	ns
VI crests ♀									.056		ns	ns
VI troughs ♂									1.486	1.245		ns
VI troughs ♀									.762	.616	.665	

Appendix 6.2 Anova table for analysis of *Cycloleberis* microdistribution data, Sept. - Oct. 1979. A = sex: juvenile, male, female; B = time, Sept. 1979, Oct. 1979; C = ripple position, between ripples, on ripples; D = sediment depth inhabited, 0 - 20, 20 - 60, 60 - 100, 100 - 140 mm.

Source of variation		df	SS	MS	F_s
A	sex	3	.8196	.2732	3.543
B	time	1	.0418	.0418	<1
C	ripple position	1	.1438	.1438	1.865
D	sediment depth	3	1.2745	.4248	5.510*
A x B		3	.0329	.0110	<1
A x C		3	.1574	.0525	<1
A x D		9	.5140	.0571	<1
B x C		1	.0235	.0235	<1
B x D		3	.0610	.0203	<1
C x D		3	.0686	.0229	<1
A x B x C		3	.1225	.0408	<1
A x B x D		9	.2128	.0236	<1
A x C x D		9	.4077	.0453	<1
B x C x D		3	.0945	.0315	<1
A x B x C x D		9	.6935	.0771	

*, p = .01 - .05; **, p = .001 - .01; ***, p <.001.

Appendix 6.3 Anova table for analysis of *Hippomedon* microdistribution data, Sept. - Oct. 1979.

Source of variation		df	SS	MS	F_s
A	sex	2	1.1728	.5864	11.148**
B	time	1	.5994	.5994	11.395*
C	ripple position	1	1.3078	1.3078	24.863**
D	sediment depth	3	1.6511	.5504	10.464**
A x B		2	.0971	.0485	<1
A x C		2	.0416	.0208	<1
A x D		6	1.9346	.3224	6.129*
B x C		1	.0270	.0270	<1
B x D		3	.4427	.1476	2.806
C x D		3	.7582	.2527	4.804*
A x B x C		2	.1787	.0894	1.700
A x B x D		6	.4341	.0723	1.375
A x C x D		6	.2217	.0370	<1
B x C x D		3	.0211	.0070	<1
A x B x C x D		6	.3156	.0526	

*, p = .01 - .05; **, p = .001 - .01; ***, p <.001.

Appendix 6.4 Analysis of mean sediment depths inhabited by juvenile, male and female *Hippomedon* between and on ripples in Sept. - Oct. 1979.

	Depth (mm)						
	$\bar{x}$	SD	n	t	p	t	p
Juveniles							
Sept. between	30.00	23.14	35	0.526	ns		
on	25.00	17.32	4				
	29.49	22.47	39				
Oct. between	33.75	22.53	56	0.401	ns	1.121	ns
on	36.54	31.99	26				
	34.63	25.73	82				
overall	33.03	24.66	122				
Males							
Sept. between	35.37	27.59	54	4.086	<.001	6.326	<.001
on	72.11	35.68	19				
Oct. between	63.95	34.01	84	1.036	ns	1.320	ns
on	70.69	28.78	29				
	65.66	32.76	113				
Females							
Sept. between	60.59	42.64	17	0.104	ns		
on	58.57	43.37	7				
	60.00	41.91	24			0.399	ns
Oct. between	64.17	29.33	24	2.445	<.05	2.458	<.05
on	90.00	30.15	12				

Appendix 6.4 continued

t-tests of mean depths inhabited by *Hippomedon*.

	juveniles	males			females		
		Sept.		Oct.	Sept.	Oct.	
		betw.	on			betw.	on
juveniles		ns	<.001	<.001	<.01	<.001	<.001
males							
Sept. between	0.536				<.02	<.001	
on	4.606				ns		ns
Oct.	8.552					ns	<.01
females							
Sept.	3.050	2.636	1.351				
Oct. between	4.874	4.075		0.221			
on	6.341		1.497	2.636			

Appendix 6.5 Anova table for analysis of *Patuki* microdistribution data, Sept. - Oct. 1979.

Source of variation	df	SS	MS	F_s
A sex	2	.0637	.0318	1.828
B time	1	.7903	.7903	45.420***
C ripple position	1	.0010	.0010	<1
D sediment depth	3	5.5422	1.8474	106.172***
A x B	2	.1005	.0503	2.891
A x C	2	.0968	.0484	2.782
A x D	6	.4260	.0710	4.081
B x C	1	.0066	.0066	<1
B x D	3	.1710	.0570	3.276
C x D	3	.0456	.0152	<1
A x B x C	2	.6869	.3434	19.736**
A x B x D	6	.1541	.0257	1.477
A x C x D	6	.7210	.1202	6.908*
B x C x D	3	.1507	.0502	2.885
A x B x C x D	6	.1041	.0174	

*, p = .01 - .05; **, p = .001 - .01; ***, p <.001.

Appendix 6.6 Analysis of mean sediment depths inhabited by juvenile, male and female *Patuki* between and on ripples in Sept. - Oct. 1979.

	Depth (mm)						
	$\bar{x}$	SD	n	t	p	t	p
Juveniles							
Sept. between	25.2	32.95	25	0.154	ns		
on	26.47	20.29	17				
	25.71	28.21	42				
Oct. between	35.51	33.67	49	0.873	ns	1.239	ns
on	30.39	24.17	52				
	32.87	29.13	101				
overall	26.01	23.14	143				
Males							
Sept. between	23.24	21.98	34	0.552	ns		
on	28.52	38.71	17				
	25.39	28.18	52				
Oct. between	25.43	21.87	35	0.901	ns	0.656	ns
on	30.15	30.15	66				
	28.52	27.55	101				
overall	27.57	27.76	153				
Females							
Sept. between	29.0	23.31	10	1.606	ns		
on	44.29	31.91	28				
	40.26	30.36	38				
Oct. between	48.39	38.32	31	0.473	ns	0.898	ns
on	43.68	30.95	19				
	46.60	35.78	50				
overall	43.86	33.51	88				

Appendix 6.7 Anova table for *Metaphoxus* microdistribution data, Sept. - Oct. 1979.

Source of variation	df	SS	MS	F_s
A sex	2	.0496	.0248	1.580
B time	1	.1536	.1536	9.783*
C ripple position	1	.2189	.2189	13.943**
D sediment depth	3	2.9300	.9767	62.210***
A x B	2	.1344	.0672	4.280
A x C	2	.5170	.2585	16.465**
A x D	6	.6875	.1146	7.299*
B x C	1	.0874	.0874	5.567
B x D	3	.3228	.1076	6.854*
C x D	3	.0189	.0063	<1
A x B x C	2	.1920	.0960	6.115*
A x B x D	6	.5165	.0861	5.484*
A x C x D	6	.0697	.0116	<1
B x C x D	3	.0673	.0224	1.427
A x B x C x D	6	.0941	.0157	

*, p = .01 - .05; **, p = .001 - .01; ***, p <.001.

Appendix 6.8 Analysis of mean sediment depths inhabited by juvenile, male and female *Metaphoxus* between and on ripples in Sept. - Oct. 1979.

	Depth (mm)						
	$\bar{x}$	SD	n	t	p	t	p
Juveniles							
Sept. between	36.55	33.52	29	0.532	ns		
on	44.44	40.35	9				
	38.42	34.84	38				
Oct. between	24.44	23.41	45	0.506	ns	2.509	<.05
on	22.14	21.80	56				
	23.17	22.45	101				
Males							
Sept. between	35.0	42.61	20	0.989	ns		
on	48.95	45.33	19				
	41.79	43.94	39				
Oct. between	39.44	32.08	18	0.191	ns	0.127	ns
on	41.20	37.18	50				
	40.74	35.67	68				
overall	41.12	38.69	107				
Females							
Sept. between	38.82	30.60	17	1.157	ns		
on	49.36	35.74	46				
	46.51	34.51	63				
Oct. between	50.59	38.97	17	0.184	ns	0.420	ns
on	48.57	32.91	35				
	49.23	34.63	52				
overall	48.07	34.41	114				

Appendix 6.9 Anova table for *Paraphoxus* microdistribution data, Sept. - Oct. 1979

Source of variation	df	SS	MS	F_s
A sex	2	.6832	.3416	11.055**
B time	1	.1192	.1192	3.858
C ripple position	1	.3805	.3805	12.314*
D sediment depth	3	.3411	.1137	3.680
A x B	2	.2816	.1408	4.557
A x C	2	.0023	.0011	<1
A x D	6	1.9559	.3260	10.550**
B x C	1	.0725	.0725	2.346
B x D	3	.2170	.0723	2.340
C x D	3	.1073	.0358	1.159
A x B x C	2	.1971	.0986	3.191
A x B x D	6	.4754	.0792	2.563
A x C x D	6	.4734	.0789	2.553
B x C x D	3	.1938	.0646	2.091
A x B x C x D	6	.1854	.0309	

*, p = .01 - .05; **, p = .001 - .01; ***, p ≤.001.

Appendix 6.10 Analysis of mean sediment depths inhabited by juvenile, male and female *Paraphoxus* between and on ripples in Sept. - Oct. 1979.

	Depth (mm)						
	$\bar{x}$	SD	n	t	p	t	p
Juveniles							
Sept. between	13.33	10.0	9	2.760	<.05	1.226	ns
on	62.50	35.0	4				
Oct. between	15.0	11.68	12	0.943	ns	2.497	<.05
on	19.20	20.58	50				
	18.39	19.18	62				
Males							
Sept. between	40.0	-	1				
on	80.0	40.0	3				
	70.0	38.30	4				
Oct. between	0		0			1.342	ns
on	100.0	23.09	4				
overall	85.0	33.38	8				
Females							
Sept. between	60.0	28.28	2				
on	60.0	30.24	8				
	60.0	28.28	10				
Oct. between	90.0	20.0	4				
on	52.0	47.65	5	1.614	ns	0.544	ns
	68.89	41.06	9				
overall	64.21	34.21	19				

Appendix 7.1 Significance of changes in instar frequencies in control and recolonized populations of *Cyclocleberis*.

P / χ^2	0 control	1	4	8	16	26	26 control
0 control		<.001	<.001	<.001	<.001	<.001	<.001
1	3134.678		<.001				<.001
4	881.976	232.709		<.005			<.001
8	1599.419		27.157		<.001		<.001
16	364.737			213.020		<.001	<.001
26	463.978				27.877		<.001
26 control	43.599	1445.496	256.666	189.117	79.128	120.208	

Appendix 7.2 Significance of differences in structures of control and recolonized populations of *Cycloleberis*, *Hippomedon*, *Patuki*, *Metaphoxus* and *Paraphoxus* (Chi square tests). Underlined values not significant ($p > .05$).

	Cycloleberis	*Hippomedon*	*Patuki*	*Metaphoxus*	*Paraphoxus*
Nov. C x Nov. 1D	2138.74	6.99	11.42	18.87	153.86
Dec. C x Dec. 1D	2178.02	19.36	105.91	55.23	20.96
Jan. C x Jan. 1D	424.37	2.398	9284.9	41.18	79.09
Feb. C x Feb. 1D	105.73	8.213	3.211	21.61	223.26
Nov. 1D x Dec. 1D	160.89	10.60	3.133	4.000	32.33
Nov. 1D x Jan. 1D	499.27	32.80	6699.68	4.000	60.94
Nov. 1D x Feb. 1D	599.42	17.60	3.000	4.000	23.95
Dec. 1D x Jan. 1D	298.88	67.69	7271.11	2.000	18.78
Dec. 1D x Feb. 1D	337.45	33.06	2.182	2.000	14.67
Jan. 1D x Feb. 1D	24.22	4.594	1.000	2.000	1.474
Dec. 26D x Dec. C	157.47	9.567	193.14	94.43	9.086
Dec. 26D x Nov. C	526.59	95.89	95.87	103.29	23.19
Feb. 28D x Feb. C	122.46	31.80	109.61	499.88	118.04
Feb. 28D x Jan. C	937.37	7.559	276.32	470.12	33.79
Mar. 27D x Mar. C	35.35	10.05	11.26	230.11	30.89
Mar. 27D x Feb. C	1001.18	48.66	80.37	63.29	331.23
Apr. 32D x Apr. C	19.85	-	-	-	4.818

Appendix 7.2 continued

	Cycloleberis	*Hippomedon*	*Patuki*	*Metaphoxus*	*Paraphoxus*
Apr. 32D x Mar. C	28.47	-	-	-	1.837
May 39D x May C	47.03	-	-	-	28.20
Dec. 26D x Feb. 28D	760.83	135.28	97.44	13.45	81.03
Dec. 26D x Mar. 27D	561.49	144.48	21.63	6.500	238.42
Dec. 26D x Apr. 32D	577.89	116.55	36.55	30.60	58.71
Dec. 26D x May 39D	494.20	721.39	24.70	35.67	374.95
Feb. 28D x Mar. 27D	964.19	21.68	21.45	6.917	6.905
Feb. 28D x Apr. 32D	1206.67	21.42	37.82	24.27	2.480
Feb. 28D x May 39D	669.34	58.05	29.64	27.54	15.80
Mar. 27D x Apr. 32D	222.78	1.995	7.637	3.539	30.71
Mar. 27D x May 39D	250.29	29.22	9.043	4.205	15.74
Apr. 32D x May 39D	61.22	42.25	1.622	1.111	28.34
degrees of freedom	9	2	2	2	2
χ^2 (.05)	16.919	5.991	5.991	5.991	5.991

Appendix 7.3 Significance of changes in composition of control and recolonized populations of *Hippomedon*, Nov. - Dec. 1979.

χ^2 \ P	0 control	1	4	8	16	26	26 control
0 control		<.05	ns	<.001	<.05	<.001	<.001
1	7.857		ns				<.001
4	1.324	3.298		<.001			<.001
8	85.233		84.937		<.001		<.05
16	7.239			20.743		<.001	<.001
26	123.037				105.849		ns
26 control	36.997	69.903	39.655	6.329	35.111	3.583	

Appendix 7.4 Significance of differences in mean sizes of juveniles, males and females in control and recolonized populations of *Hippomedon* (data from Table 11.3).

Juveniles

t \ P	0 control	1	4	8	16	26	26 control
0 control		<.001	<.01	<.001	<.01	<.001	<.01
1	3.741		ns				ns
4	2.880	0.585		ns			ns
8	3.477		0.203		ns		ns
16	2.773			0.673		.02<p<.01	ns
26	5.664				2.334		<.001
26 control	3.282	1.814	0.995	1.398	0.582	3.571	

Males

t \ P	0 control	1	4	8	16	26	26 control
0 control		ns	ns	<.05	ns	ns	<.01
1	0.399		ns				<.05
4	1.150	0.749		ns			ns
8	2.027		1.580		ns		<.01
16	0.431			0.140		ns	<.01
26	0.589				0.142		<.01
26 control	2.748	2.076	1.015	3.231	3.070	3.281	

Appendix 7.4 continued

t \ P	0 control	1	4	8	16	26	26 control
				Females			
0 control		ns	ns	ns	ns	ns	ns
1	0		ns				ns
4	0.932	1.331		ns			ns
8	0.092		0.430		ns		ns
16	1.265			0.578		ns	ns
26	0.154				0.654		ns
26 control	0.402	0.438	0.173	0.314	0.446	0.214	

Appendix 7.5 Significance of differences (t-tests) in mean sizes of juveniles, males and females of the four amphipods in control and recolonized populations (* = p <.05, ** = p <.01, *** = p <.001).

	Hippomedon			*Patuki*			*Metaphoxus*			*Paraphoxus*		
	juv.	♂	♀	juv.	♂	♀	juv.	♂	♀	juv.	♂	♀
Nov. C x Nov. 1D	*** 3.740	.399	0	1.626	-	-	-	-	-	.494	.445	* 2.598
Dec. C x Dec. 1D	** 3.233	** 2.632	1.391	*** 4.252	* 2.018	* 2.318	-	1.747	-	1.401	.453	.285
Jan. C x Jan. 1D	.979	0	1.429	-	-	-	-	-	-	1.072	-	*** 5.382
Feb. C x Feb. 1D	.345	.840	1.083	-	-	-	-	1.642	-	.596	-	2.152
Dec. 26D x Nov. C	*** 5.664	.589	.154	.237	.243	.374	.103	.046	1.687	1.930	* 2.580	*** 4.792
Dec. 26D x Dec. C	*** 3.571	** 3.281	.215	.641	.848	1.839	0	.461	* 2.646	.304	1.328	1.363
Feb. 28D x Jan. C	.662	.934	1.800	* 2.770	1.972	-	** 2.691	-	.206	1.677	-	** 2.818
Feb. 28D x Feb. C	0	1.922	.308	*** 5.071	1.784	-	.825	-	.641	1.495	-	.948
Mar. 27D x Feb. C	* 2.247	.142	.633	1.757	*** 3.739	.086	.047	-	1.013	*** 4.425	.414	.776
Mar. 27D x Mar. C	1.403	.529	.326	.401	.805	** 3.292	.082	-	* 2.167	* 2.661	.545	1.666

*, p = .01 - .05; **, .001 - .01; ***, p <.001.

Appendix 7.6 Significance of changes in composition of control and recolonized populations of *Patuki*, Nov. - Dec. 1979.

χ^2 \ P	0 control	1	4	8	16	26	26 control
0 control		<.01	<.001	<.01	<.001	<.001	ns
1	12.119		<.001				<.001
4	27.060	22.222		<.001			<.01
8	11.071		81.165		<.001		<.001
16	169.553			196.003		ns	<.001
26	123.159				5.784		<.001
26 control	4.905	48.820	10.839	22.682	185.229	181.635	

Appendix 7.7 Significance of differences in mean sizes of juveniles, males and females in control and recolonized populations of *Patuki* (data from Table 11.5).

Juveniles

t \ P	0 control	1	4	8	16	26	26 control
0 control		ns	<.001	ns	ns	ns	<.05
1	1.626		ns				ns
4	6.111	0.273		<.001			<.001
8	0.770		6.301		ns		<.01
16	0.782			1.281		ns	ns
26	0.237				0.216		ns
26 control	2.415	1.377	5.383	2.875	0.682	0.641	

Males

t \ P	0 control	1	4	8	16	26	26 control
0 control		-	<.01	<.001	ns	ns	ns
1	-		-				-
4	3.482	-		ns			<.05
8	3.816		0.616		<.001		<.001
16	0.578			4.527		ns	ns
26	0.203				0.936		ns
26 control	0.472	-	2.497	5.385	0.207	0.848	

Appendix 7.7 continued

t \ p	Females						
	0 control	1	4	8	16	26	26 control
0 control		-	-	<.001	ns	ns	ns
1	-		-				-
4	-	-		-			-
8	7.121		-		<.001		<.001
16	1.697			6.100		ns	<.01
26	0.756				1.017		ns
26 control	0.992	-	-	8.457	2.816	1.839	

Appendix 7.8 Significance of changes in composition of control and recolonized populations of *Metaphoxus*, Nov. - Dec. 1979.

χ^2 \ P	0 control	1	4	8	16	26	26 control
0 control		<.001	<.001	ns	ns	<.001	ns
1	10155.451		<.001				<.001
4	8542.043	51.250		<.001			<.001
8	4.160		160.0		<.001		<.01
16	4.056			17.316		<.001	ns
26	120.553				72.155		<.001
26 control	3.861	500.525	280.145	13.008	3.847	75.642	

Appendix 7.9 Significance of differences in mean sizes of juveniles, males and females in control and recolonized populations of *Metaphoxus* (data from Table 11.7).

Juveniles

t \ p	0 control	1	4	8	16	26	26 control
0 control		-	-	ns	<.05	<.05	<.01
1	-		-				-
4	-	-		-			-
8	1.143		-		ns		ns
16	2.189			1.148		ns	ns
26	2.466				0		ns
26 control	2.865	-	-	1.220	0	0	

Males

t \ p	0 control	1	4	8	16	26	26 control
0 control		-	-	<.001	ns	ns	ns
1	-		-				-
4	-	-		-			-
8	3.762		-		ns		<.05
16	1.991			0.293		ns	ns
26	0.046				1.026		ns
26 control	1.202	-	-	2.085	1.214	0.461	

Appendix 7.9 continued

t \ p	Females						
	0 control	1	4	8	16	26	26 control
0 control		-	ns	ns	ns	ns	<.05
1	-		-				-
4	1.495	-		ns			ns
8	0.545		0.717		ns		ns
16	0.191			0.585		ns	ns
26	1.705				1.229		<.01
26 control	2.107	-	0.804	0.161	1.358	2.672	

Appendix 7.10 Significance of changes in composition of control and recolonized populations of *Paraphoxus*, Nov. - Dec. 1979.

χ^2 \ P	0 control	1	4	8	16	26	26 control
0 control		<.001	<.001	<.001	<.05	<.001	<.001
1	296.586		<.001				<.001
4	31.367	532.277		<.001			<.001
8	17.275		150.744		ns		ns
16	9.172			1.350		<.01	<.01
26	20.386				9.680		ns
26 control	29.018	681.266	245.058	4.782	11.207	5.836	

Appendix 7.11 Significance of differences in mean sizes of juveniles, males and females in control and recolonized populations of *Paraphoxus* (data from Table 11.9).

Juveniles

t \ p	0 control	1	4	8	16	26	26 control
0 control		ns	ns	ns	<.001	ns	<.05
1	0.494		ns				<.05
4	0.750	1.031		ns			ns
8	0.076		0.818		<.001		<.05
16	3.750			3.893		<.05	<.05
26	1.930				2.307		ns
26 control	2.256	2.165	0.865	2.430	2.098	0.304	

Males

t \ p	0 control	1	4	8	16	26	26 control
0 control		ns	<.001	<.05	ns	<.05	ns
1	0.445						ns
4	7.805	2.247		ns			ns
8	2.657		0		ns		ns
16	0.356			1.497		ns	ns
26	2.580				1.386		ns
26 control	0.155	0.016	1.716	1.430	0.111	1.328	

Appendix 7.11 continued

t \ p	Females						
	0 control	1	4	8	16	26	26 control
0 control		<.05	<.05	<.01	ns	<.001	<.001
1	2.598		ns				ns
4	2.544	0.180		ns			ns
8	2.791		0.962		ns		ns
16	0.661			2.000		<.05	ns
26	4.792				2,398		ns
26 control	1.434	0.025	0.121	0.793	1.400	1.363	

Appendix 8.1 Sizes (calculated by application of growth factors) and ages (calculated using Sutcliffe & Carrick's (1981) relationship for mean moult interval) of mature female instars of the four Kaikoura amphipods.

Hippomedon $\bar{x}\ M_i = 7.5e^{.008t}$

instar size	age(d)	M_i(d)
.356	84	14.7
.377	98.7	16.5
.400	115.2	18.8
.424	134.1	21.9
.449	156.0	26.1
.476	182.0	32.2
.505	214.2	41.6
.535	255.8	

estimated maximum longevity = 260d

Metaphoxus $\bar{x}\ M_i = 7.5e^{.008t}$

instar size	age(d)	M_i(d)
.588	90	15.4
.623	105.4	17.4
.660	122.8	20.0
.700	142.9	23.5
.742	166.4	28.4
.786	194.8	35.6
.833	230.4	

estimated maximum logevity = 242d

Appendix 8.1 continued.

Patuki $\bar{x}\ M_i = 7.5e^{.008t}$

instar size	age(d)	M_i(d)
.796	56	7.5
.843	63.5	12.5
.894	76.0	13.8
.948	89.7	15.4
1.005	105.1	17.4
1.065	122.5	20.0
1.129	142.5	23.5
1.196	165.9	28.5
1.268	194.2	35.5
1.344	229.7	47.1
1.425	276.8	

estimated maximum longevity = 271d

Paraphoxus $\bar{x}\ M_i = 3.8e^{.008t}$

instar size	age(d)	M_i(d)
1.096	164	14.1
1.162	178.1	15.8
1.231	193.9	17.9
1.305	211.8	20.7
1.384	232.5	24.4
1.467	256.9	29.7
1.554	286.6	37.6
1.648	324.3	50.9
1.747	375.1	76.4
1.851	451.5	
1.963	individuals in this size range	
2.080	belonged to cohorts originating	
2.205	before commencement of study.	

estimated longevity (to 1.850 mm h.l.) = 434d.

Appendix 8.2 Net reproduction rates (R_0) of the five Kaikoura crustaceans using embryo sex ratios of 1:1. n_x, number of females surviving to instar x (from Figs. 12.1a-d); l_x, proportions of female embryos surviving to instar x; m_x, female offspring produced per female in instar x (from female size - brood size regressions, Chapters 5 - 8).

Hippomedon

instar size (h.l., mm)	age(d)	n_x	l_x	m_x	$l_x m_x$
.356	84	142.5	.355	.831	.295
.377	99	118.8	.296	1.056	.313
.400	115	88.8	.221	1.302	.288
.424	134	116.25	.290	1.559	.452
.449	156	32.8	.082	1.827	.149
.476	182	31.3	.078	2.117	.165
.505	214	3.1	.008	2.427	.019
.535	256	2.5	.006	2.750	.017
					1.698
				14.2% brood mortality	- .241
				R_0 =	1.457

G = .399y

r = 0.945 per individual per year

Appendix 8.2 continued

Metaphoxus

instar size (h.l., mm)	age(d)	n_x	l_x	m_x	$l_x m_x$
.588	90	71.3	.285	.230	.066
.623	105	88.8	.355	.565	.201
.660	123	121.3	.485	.918	.445
.700	143	123.8	.495	1.301	.644
.742	166	105.6	.423	1.702	.719
.786	195	43.8	.175	2.123	.372
.833	230	21.9	.088	2.572	.225
				9.411	2.672
				30.4% brood mortality	- .812
				R_0 =	1.860

G = .617y

r = 1.006 per individual per year

Appendix 8.2 continued

Patuki

instar size (h.l., mm)	age(d)	n_x	l_x	m_x	$l_x m_x$
.796	56	130	.187	.794	.148
.843	64	184.4	.265	1.371	.363
.894	76	72.5	.104	1.998	.208
.948	90	68.8	.099	2.661	.263
1.005	105	40	.057	3.361	.193
1.065	123	25.6	.037	4.098	.151
1.129	143	23.1	.033	4.884	.162
1.196	166	10.6	.015	5.707	.087
1.268	194	1.5	.002	6.592	.014
1.344	230	1.1	.002	7.525	.014
1.425	277	1.0	.001	8.520	.012
				47.511	1.615

zero brood mortality

R_o = 1.615

G = .431y

r = 1.112 per individual per year

Appendix 8.2 continued

Paraphoxus			1978 - 79			1979 - 80		
instar size (h.l., mm)	age(d)	m_x	n_x	l_x	$l_x m_x$	n_x	l_x	$l_x m_x$
1.096	164	8.115	50	.055	.448	21.3	.033	.271
1.162	178	8.713	51.3	.057	.493	20.0	.031	.274
1.231	194	9.337	31.3	.035	.322	22.5	.035	.330
1.305	212	10.007	18.1	.020	.200	20.6	.032	.325
1.384	233	10.722	10.6	.012	.126	21.3	.033	.358
1.467	257	11.473	3.6	.004	.046	6.9	.011	.124
1.554	287	12.261	1.9	.002	.025	2.3	.004	.043
1.648	324	13.111						
1.747	375	14.007	1.9	.002	.028			
1.851	452	14.949						
					1.688			1.725
		34.5% brood mortality			- .582			- .595
					R_0 = 1.106			R_0 = 1.130
					G = .807y			G = .860y
		r = .125 per individual per year						r = .142

Appendix 8.3 Dry weights of females (recently matured) and their eggs for each of the South Bay crustaceans. Samples of embryos and females oven dried at 80°C for 72 h and weighed to nearest 0.001 mg using a Kahn microbalance.

	Dry weight ♀ (mg)		Dry weight eggs (mg)	
	$\bar{x}$	n	$\bar{x}$	n
Hippomedon	0.604	9	0.0192	4
Patuki	1.662	1	0.0269	6
Metaphoxus		0	0.0127	1
Paraphoxus	1.236	2	0.0244	7
Cycloleberis	15.480	7	0.1097	7